Hyporheic Ecology of Alluvial Rivers in Canterbury, New Zealand

A thesis

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"They are found ... in the waters on the earth and in the dark recesses of caverns and of the waters under the earth, where no storm ruffles the everlasting stillness, no light illumines the thick darkness, and no sound breaks the eternal silence."

Charles Chilton, 1894

Contents

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Abstract

Aspects of the ecology of hyporheic river communities in Canterbury, New Zealand were examined using field surveys in association with field and laboratory experiments. Seasonal pump-sampling of Ashley River tributaries revealed an invertebrate fauna dominated numerically by harpacticoid copepods, although insects (particularly Chironomidae and Polycentropodidae) dominated biomass. Dissolved oxygen (minimum concentration = 2.1 mg l^{-1}) was negatively related to invertebrate abundance in reaches receiving upwelling groundwater in summer, but not winter. Thus, seasonal limitation of dissolved oxygen may occur in river reaches where upwelling is prevalent. Colonisation pots embedded in the Waipara River collected a high proportion of epigean taxa, notably the snail *Potamopyrgus antipodarum*, whereas pump-samples were biased towards collecting non-insect taxa, including harpacticoids and mites. In colonisation pots, the hyporheic biota (15-45 cm depth) represented about 50% of total (0-45 cm) invertebrate abundance and community respiration. Willow leaves added to colonisation pot gravels increased invertebrate abundance and community respiration, but their effect declined with depth. Low concentrations of silt (< 2.5 g per litre of sediment) appeared to enhance the food resource for some collector-filtering taxa (particularly oligochaetes and ostracods), whilst lessening its value to the grazers *P. antipodarum* and *Hydora* sp. (Elmidae). The epilithic microbial community found in the hyporheic zone was similar to that of heavily-shaded surface epilithon, and both had lower biomass and a less diverse microbiota (algae and fungi) than epilithon grown in full light. While the epigean caddisfly *O. feredayi* ingested hyporheic foods, it did not grow in the absence of either higher quality light-grown epilithon, or particulate organic matter. Fine sediment (< 2 mm diameter) added to colonisation pot gravels (up to 23% of total sediment dry weight) reduced invertebrate abundance and community respiration (CR) at all depths (0-45 cm). However, invertebrate community composition was influenced more strongly by fine sediment at depths below 15 cm, indicating that conventional stream sampling may provide an inadequate measure of sediment effects on the benthos. Finally, my data indicate that the hyporheic zone is likely to be sensitive to human activities. Therefore, water managers need to consider the biota of surface *and* subsurface waters concomitantly, so that freshwater ecosystems can be understood, maintained and protected, effectively.

Chapter 1

Introduction

The hyporheic zone

In many rivers and streams worldwide, surface water penetrates vertically and laterally well into the substrate. Surface water may carry nutrients, dissolved oxygen, and organic matter, which can support an abundant subsurface microbial and invertebrate community (Boulton, 2000a; Findlay & Sobczak, 2000). This subsurface region where surface water mixes with groundwater is known as the hyporheic zone (Orghidan, 1959; White, 1993). Collections of hyporheic fauna began early last century (Karaman, 1935), although detailed ecological studies have only been undertaken in the last 20-30 years (Valett et al., 1993). Many of these studies have found that with increasing distance within the bed, oxygen becomes depleted, organic matter is used up, and biological activity declines (Findlay, 1995; Boulton, 2000a; Findlay & Sobczak, 2000). Nevertheless, the hyporheic zone can contribute significantly to the metabolism of organic matter, and the transformation of nutrients in river ecosystems (Mulholland et al., 1997), and by doing so is a functionally significant component of river ecosystems (Brunke & Gonser, 1997).

Characteristics of the hyporheic zone

The dynamic ecotone model of the hyporheic zone (Gibert et al., 1990; Vervier et al., 1992) highlights the importance of the direction and rate of hydrologic exchange between surface and groundwaters to hyporheic communities. Thus, the hyporheic zone is characterized by physicochemical and biological gradients between surface and groundwater environments, and the steepness of these gradients is determined by hydrologic exchange across the ecotone.

Hydrologic exchange across the hyporheic zone may be viewed in terms of whether a stream reach is losing surface water to (downwelling), or gaining water from (upwelling) groundwater. Downwelling surface water is typically highly oxygenated, and may stimulate aerobic microbial activity and invertebrate abundance in the hyporheic zone. In contrast, upwelling groundwater typically contains less oxygen and supports a less

abundant and diverse hyporheic fauna. However, upwelling groundwater may be rich in nutrients or dissolved organic carbon (DOC) that stimulate microbial production at and near the sediment surface (Hynes, 1983).

The rate of water exchange through hyporheic sediments is determined by substrate particle size and packing, and river discharge (Brunke & Gonser, 1997). Fine sediments, such as sand, reduce interstitial flow rates, lower interstitial dissolved oxygen concentrations and may cause a rapid decline in invertebrate abundance with increasing depth (Poole & Stewart, 1976; Grimm & Fisher, 1984; Herbst, 1980). However, increased river discharge may replenish hyporheic sediments which were depleted of oxygen, increasing microbial and invertebrate activity (Boulton & Stanley, 1995; Stanley & Boulton, 1995).

Interactions between surface and subsurface waters are not limited to the region immediately below the streambed. Authors writing in a recent special issue of the journal *Freshwater Biology* (1998, volume 40, number 3) stressed that surface water may penetrate well beyond the banks of a river, and that river ecology and management should therefore take this into account. The papers in this special issue make it clear that the flow and transformation of nutrients and organic matter between a river and its floodplain are determined by geomorphological and hydrological characteristics of the catchment. Accordingly, the hyporheic fauna and microbiota will also be affected by processes both within the flowing river channel and the greater catchment. These ideas are expansions on the early writings of Hynes (1983), who called for river ecologists to become familiar with groundwater concepts and study.

DOC is supplied to sediment interstices through infiltration of surface water or groundwater (Vervier et al., 1993; Fiebig, 1995; Marmonier et al., 1995; Jones et al., 1996; Baker et al., 2000), while most particulate organic carbon (POC) probably reaches the hyporheic zone through burial during bed-moving floods (Naegeli et al., 1995; Findlay & Sobczak, 2000). Buried organic matter may become colonised by fungi and bacteria, which provide a rich source of food for hyporheic invertebrates (Herbst, 1980; Rounick & Winterbourn, 1983; Smith & Lake, 1993). Microbial biofilms may also be an important food source for hyporheic invertebrates (Bärlocher & Murdoch, 1989), although it is not known whether they are of sufficient nutritional value to support invertebrate growth.

The invertebrate fauna of the hyporheic zone is known as the hyporheos (sensu Williams & Hynes, 1974). An occasional hyporheos of epigean taxa includes many insect and mollusc taxa that spend only part of their life history in the hyporheic zone and are

more typically associated with surface sediments (Williams & Hynes, 1974). In contrast, the permanent hyporheos comprises truly hypogean taxa that spend their entire lives below the sediment surface. The permanent hyporheos includes numerous crustaceans, oligochaetes and mites (Williams & Hynes, 1974; Boulton, 2000a). Hypogean taxa are well adapted to interstitial life, and often have reduced or no eyes, reduced pigmentation, and small body size. Many are good burrowers. Hypogean taxa often tolerate lower oxygen concentrations than epigean taxa (Malard & Hervant, 1999), which enables them to colonise poorly oxygenated upwellings, or sediments where hydraulic conductivity is low (Boulton, 2000a). The proportion of insect taxa in the hyporheic zone may increase in autumn and winter (Williams & Hynes, 1974; Strommer & Smock, 1989; Marchant, 1995; Fraser & Williams, 1998), due to the hatching of eggs laid in summer (Williams & Hynes, 1974). In addition, the hyporheic zone may serve as a refuge for epigean invertebrates from flooding and drying at the substrate surface, although evidence supporting the hyporheic refuge concept remains equivocal (Palmer et al., 1992; Marchant, 1995; Clinton et al., 1996; del Rosario & Resh, 2000).

Gibert (1990) classified the faunas of flowing waters according to their affinities with groundwater. Thus, stygoxenes are epigean organisms that have no affinities with groundwater systems, but may occur 'accidentally' in the hyporheic zone. Such organsims include many insect taxa whose whole life histories are spent at or about the sediment surface. Animals that may exploit resources in both groundwater and surface water were termed stygophiles by Gibert who noted they may include occasional and permanent hyporheos. Finally, Gibert referred to members of the specialized groundwater subterranean fauna as stygobites, a group comprising ubiquitous stygobites found in all types of groundwater systems, and phreatobites, found only in deep groundwater.

Hyporheic research in New Zealand

Although the description of New Zealand's groundwater biota began over a century ago (Chilton, 1894), ecological studies of the hyporheic zone have been undertaken only in the last decade. Collier & Scarsbrook (2000) recently reviewed the New Zealand hyporheic literature, and showed that despite its infancy a diversity of hyporheic research has been accomplished. Studies in Otago (Scarsbrook, 1995; Huryn, 1996; Montgomerie, 1997; Olsen et al., 2001), Cass (McLeod, 1998; Adkins & Winterbourn, 1999; Fowler & Death,

2001), and Reefton (Anthony, 1999), in the South Island, and Whatawhata (Boulton et al., 1997; Collier & Scarsbrook, 2000) in the North Island, all report diverse hyporheic faunas.

Most New Zealand studies have found the hyporheic community dominated by insect taxa, although Scarsbrook (1995), and Anthony (1999), collected mostly hypogean crustaceans by pump-sampling. Huryn (1996) and Adkins (1997) found inclusion of the hyporheic zone improved areal estimates of benthic invertebrate production. Furthermore, Scarsbrook (1995) suggested that the hyporheic zone may be a passive refuge from flood disturbance for numerous epigean taxa in two Otago streams. However, McLeod (1998) found that the hyporheic zone (to 30 cm depth) was not a refuge from drying in an intermittent reach of Middle Bush Stream at Cass.

Montgomerie (1997) found invertebrate abundance was positively correlated with hydraulic conductivity and dissolved oxygen concentration in several Otago streams. Boulton et al (1997) suggested that sedimentation caused by forest clearance was a likely reason for lower invertebrate abundance and dissolved oxygen in the hyporheic zone of pasture streams than forested streams. In a comparison of streams affected by acid mine drainage, Anthony (1999) found a less abundant and diverse hyporheos in streams below pH 4.5.

There have been few studies of hyporheic microbial communities in New Zealand, although Rounick & Winterbourn (1983) and Tank & Winterbourn (1995; 1996) reported lower microbial activity on leaves and wood in the hyporheic zone than at the sediment surface.

'Knowledge gaps' in hyporheic ecology

Although numerous conceptual models of the hyporheic zone have been developed (e.g., Stanford & Ward, 1993; White, 1993; Hendricks, 1993; Findlay, 1995), understanding of subsurface ecological processes lags behind that of surface sediments (Stanley & Jones, 2000). This is be due in part to the relative newness of the subject and the sheer difficulty of sampling below the sediment surface, particularly in coarse sediments and large rivers. Furthermore, sampling methods that can be used in one stream type may be inappropriate in another (e.g., coring in sandy versus coarse sediments), confounding cross-site comparisons. In fact, few cross-site ecological studies have been made using the same sampling method (Stanley & Jones, 2000), and little is known of how seasonal variations in flow may influence vertical hydrologic exchange and hyporheic biota (Franken et al.,

2001). Few field experiments have been done in the hyporheic zone, but are essential for empirical hypothesis-testing of survey results (Palmer, 1993).

The ecology of hyporheic microbial communities is more poorly understood than invertebrates, although microbes are likely to be important in nutrient and organic matter transformations, as well as being sources of food for hyporheic invertebrates (Findlay & Sobczak, 2000). Also, few studies have investigated the impact of human activities, such as flow regulation or increased sedimentation, on hyporheic communities, either invertebrate or microbial (Gibert et al., 1997; Boulton, 2000b). However, several studies suggest the hyporheic zone is sensitive to sedimentation (Richards & Bacon, 1994; Boulton et al., 1997), increased salinity (Boulton et al., 1999), paper mill discharges (Lafont et al., 1996), and heavy metal toxicity (Gibert et al., 1995).

Aims and scope of the thesis

The sequence of chapters in this thesis follow a progression from hyporheic surveys (Chapters 2 and 3) to field and laboratory experiments (Chapters 4-6) designed to test hypotheses generated from my field surveys and those of others. **The general aim of the thesis is to determine what factors *cause* patterns of hyporheic community structure observed in the field.** Chapters are written in the style of 'stand alone' scientific papers, intended for publication. For this reason, there is some overlap and repetition in their introductions and discussions. However, I have attempted to present them as a logical progression of ideas with minimal redundancy.

In **Chapter 2**, a survey of the hyporheos of three rivers draining the Canterbury foothills was undertaken by pump-sampling (Figure 1). The aim of the study was to compare the relative influence of the direction of vertical hydrologic exchange and season on the hyporheos. Results from Chapter 2 suggest that while the vertical hydraulic gradient (VHG) may be seasonally important in river reaches containing upwelling and downwelling conditions, other factors may be more important in predominantly downwelling, or lowland reaches. **Chapter 3** describes a seasonal survey of the hyporheos at 8 lowland sites on the Waipara River (Figure 2) to test this prediction. In the Waipara, colonisation pots (Figure 3) supplemented seasonal pump-sampling, and provided information on the depth distribution (to 45 cm) of invertebrates, organic matter, fine sediments and community respiration (CR).

Results from the Waipara survey suggested that hyporheic invertebrates and community respiration may be limited by food availability. This hypothesis is examined in **Chapter 4**, which reports a field experiment undertaken in the Waipara where colonisation pot sediments were seeded with willow leaves as a carbon source.

While Chapter 4 considers community-level responses to hyporheic food availability, **Chapter 5** examines larval growth of a common caddisfly *Olinga feredayi* (Conoesucidae) in mesocosms (Figure 4) containing different surface and hyporheic foods. *O. feredayi* is commonly found in the hyporheic zone of New Zealand rivers (Collier & Scarsbrook, 2000), and has been variously described as a shredder or collector-browser (Winterbourn, 2000).

The Waipara survey also indicated that high concentrations of fine sediment may result in reductions of hyporheic invertebrate abundance and community respiration. **Chapter 6** therefore describes a field experiment designed to examine these relationships more specifically by adding various concentrations (0-45% of total dry weight) of fine sediment to colonisation pots buried in the Waipara River.

Two other field experiments were established, but because they were not completed successfully, are not reported in this thesis. Briefly, the first experiment sought to determine whether the addition of leaves to colonisation pot substrates would stimulate invertebrate abundance and CR equally at different depths and in upwelling and downwelling zones of a Canterbury river (the Glentui). The experiment involved digging 24 colonisation pots into the Glentui, but ended prematurely when a flood relocated or buried all but 6 of the pots. The second (failed) field experiment sought to determine how addition of nutrients (NPK fertilizer pellets) and leaves to colonisation pot substrates, would influence invertebrate abundance and CR at different depths in the substrate of the Waipara. Again, a flood occurred during the experiment, and after many hours of data analysis I concluded that the data were of little value, due to insufficient leaf material remaining, and the confounding effects of scour on experimental treatments. These thwarted experiments highlight the challenge of sampling and conducting field experiments in the hyporheic zone of streams in an unpredictable climate.

Chapter 7 summarizes and discusses my overall findings.

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Garry River - upper reach (18 m wide)

- lower reach (18 m wide)

Grey River - upper reach (8 m wide)

- lower reach (10 m wide)

Glentui River - upper reach (8 m wide)

- lower reach (28 m wide)

Figure 1. Upper (*left*) and lower (*right*) reaches of the Garry, Grey and Glentui Rivers (see Chapter 2). All photographs were taken during summer 1998, except the image of the upper Garry River, which was taken in winter 1998. Values in parentheses are mean widths of the non-vegetated channel.

Figure 2. The Waipara River, flowing from the top of the photograph. Site 7 (Chapter 3) was at the head of the riffle shown, and field experiments (Chapters 4 & 6) were conducted a further 50 m upstream. Width of the riffle was 10-15 m.

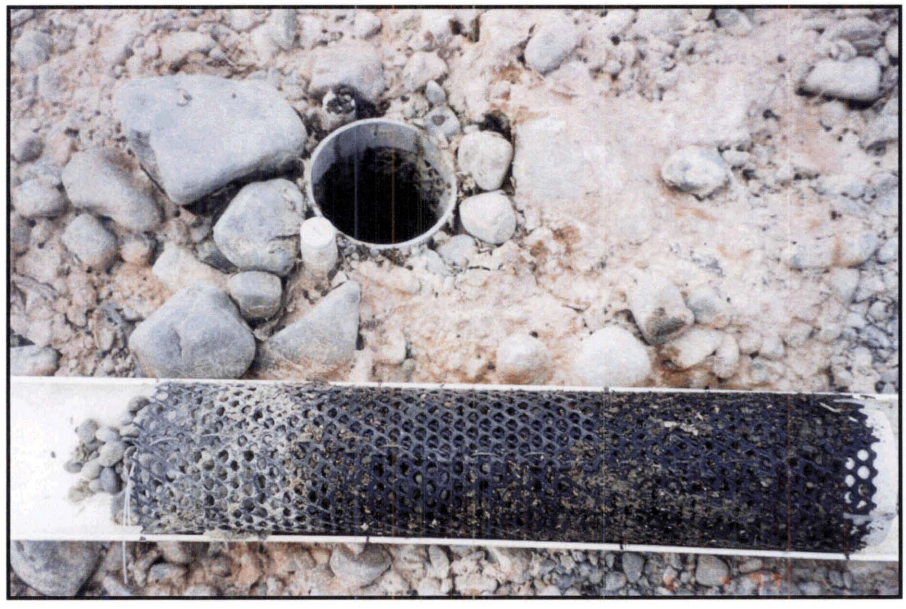

Figure 3. A colonisation pot (diameter = 11 cm) at Site 1 in the Waipara River, taken when surface water was absent (Chapter 3). The upper 10-15 cm of the sediment was dry (left end of the sediment-filled core above).

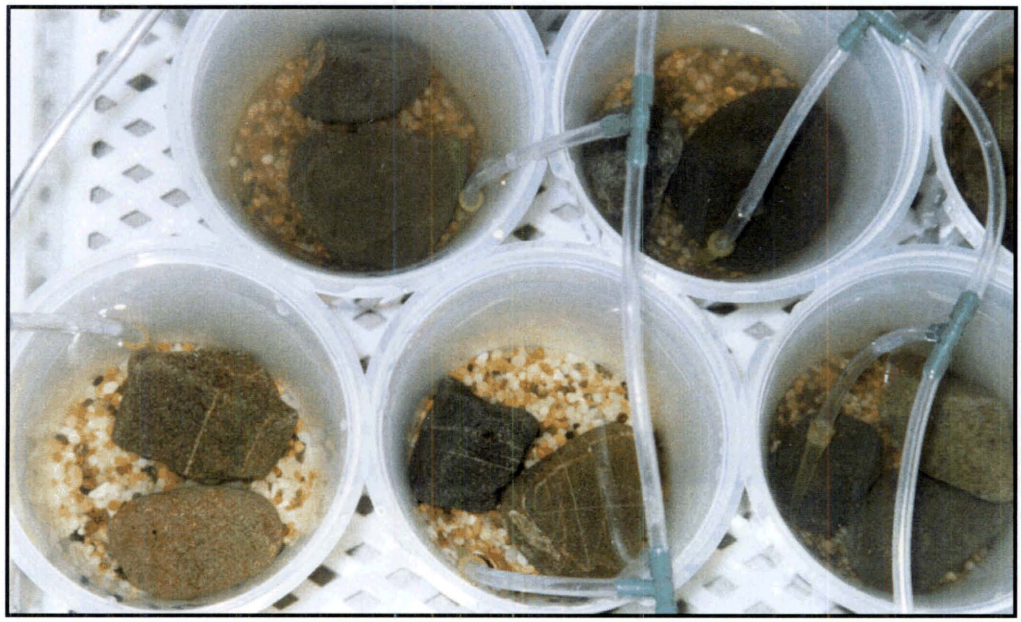

Figure 4. Mesocosms used for the *Olinga feredayi* growth experiment (Chapter 5). Mesocosms along the top and right side of the image contain fine particulate matter (FPOM), making them appear darker than the two that lack FPOM (at bottom left and centre).

Chapter 2

Seasonal differences in the effects of hydrology on hyporheic invertebrate communities

Introduction

Water exchange between the stream surface and subsurface exerts a primary influence on the ecology of subsurface, or hyporheic, stream communities (Brunke & Gonser, 1997). Downwelling surface water may bring oxygen and food to hyporheic invertebrates (the hyporheos, sensu Williams & Hynes, 1974), while upwellings are often poorly oxygenated, and contain a lower abundance and diversity of invertebrates (Boulton et al., 1998). Differences in hydrologic exchange occur across a range of scales, from catchment to sediment patches (Gibert et al., 1994; Boulton et al., 1998) and are brought about by changes in catchment geomorphology and streambed topography.

The degree of surface-subsurface hydrologic exchange is also limited by stream discharge and streambed porosity, a function of sediment particle size and packing (Freeze & Cherry, 1979). Hydrologic exchange occurs at a slower rate at low discharge, or in very fine sediments, and results in less penetration of oxygenated surface water into the hyporheic zone (Whitman & Clark, 1982; Strommer & Smock, 1989; Angradi & Hood, 1998). Reduced hydrologic exchange and lowered interstitial dissolved oxygen (DO), due to deposition of fine sediment, are likely reasons for lower species richness of the hyporheos in pasture streams compared to native forest streams (Boulton et al., 1997).

High discharge and low water temperatures during winter typically are associated with higher interstitial DO concentrations in winter than in summer (Williams & Hynes, 1974; Whitman & Clark, 1982; Strommer & Smock, 1989; Fraser & Williams, 1998). Thus, DO may be seasonally limiting to the hyporheos. As hyporheic DO is also affected by the vertical hydraulic gradient (VHG), seasonal variation in the influence of VHG on hyporheic communities may be expected. However, the relative influence of season and VHG on the hyporheos has not been examined explicitly.

Numerous rivers draining the foothills of Canterbury become dry as they reach the highly permeable glacial outwash of the Canterbury Plains (Canterbury Regional Council 1996). Lower reaches, where flow becomes intermittent, are dominated by strong downwelling, while flow in upstream reaches is maintained by upwelling groundwater during summer baseflow conditions (Anderson, 1994). These conditions make it easy to identify stream reaches of differing hydrology and allow replication of hydrologic conditions possible at the river segment scale.

In this chapter, I make seasonal comparisons of the physicochemistry and hyporheos of upper and lower reaches of three intermittent Canterbury rivers. As upper and lower reaches were expected to be relatively upwelling and downwelling, respectively, I predicted that differences in VHG would result in distinct faunas in these reaches. I also predicted that the negative influence of upwellings on invertebrate abundance would be greatest during low flow conditions in summer, and least during high flow conditions in winter.

Methods

Study Sites

The Garry, Grey and Glentui rivers are tributaries of the Ashley River on the East Coast of the South Island (Figure 1). The headwaters of these rivers arise in mountain beech (*Nothofagus solandri* Hook) forest and their lower reaches flow intermittently across the alluvial Canterbury Plains. Flow in upstream reaches is maintained by groundwater discharge at times of low rainfall in summer. There are no significant (> 1 l/s) surface or groundwater abstractions upstream of the reaches studied. Therefore, flow intermittency must be a natural phenomenon in these rivers and is most likely caused by a combination of low rainfall, low groundwater levels and coarse, permeable substrata.

In each of the three rivers, two 100 m reaches were sampled: an upper, perennially flowing reach, and a lower, intermittent reach. Lower and upper reaches were about 600-2000 m apart. All reaches were relatively open, except the upper Glentui reach, which was slightly narrower than the others (Table 1) and had some overhanging vegetation (predominantly *Salix* spp., *Coriaria arborea* and *Coprosma* spp.).

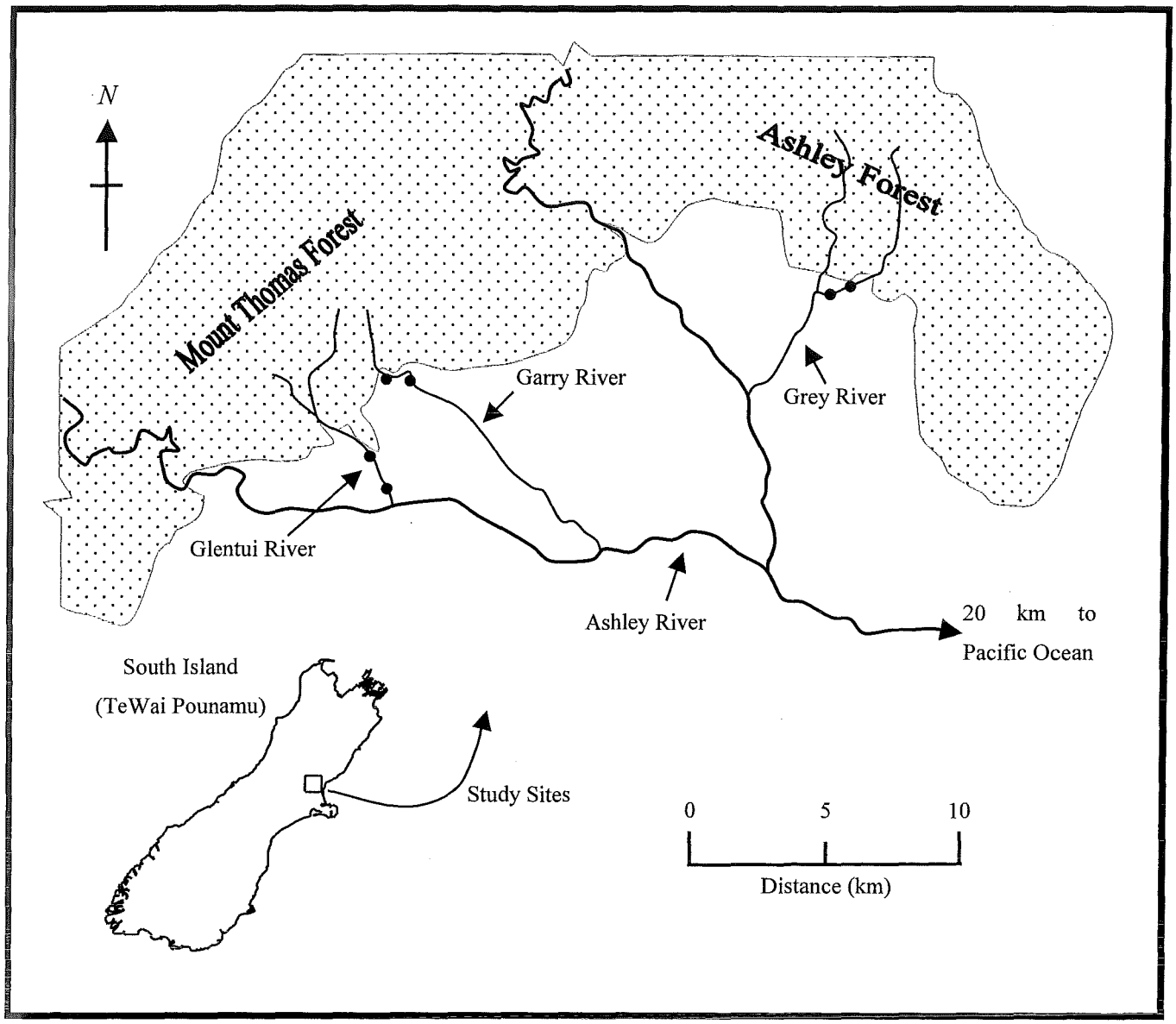

Figure 1. The Garry, Grey and Glentui Rivers, with the location of study reaches shown (•). Flow in the Ashley River is from left to right.

Table 1. Site characteristics of the rivers and study reaches. ¶ Ratio between wetted channel and total, non-vegetated channel width.

Variable	Garry River		Grey River		Glentui River	
	Upper	Lower	Upper	Lower	Upper	Lower
Latitude & Longitude	172°18' E, 42°12' S		172°30' E, 43°10' S		172°18' E, 43°14' S	
Mean Depth (m)	0.16	0.15	0.14	0.14	0.12	0.11
Mean Wetted Width (m)	7.73	8.72	6.5	5.29	3.82	3.81
Wet : Dry Width ¶	0.45	0.47	0.68	0.66	0.55	0.15
Mean Discharge (m^3 s^{-1})	0.42		0.23		0.13	

Surface substrate composition was determined at each reach by measuring stone widths (nearest mm) at regular intervals across 10 cross-sections, so that a total of 100 stones were measured at each reach. At each cross-section, the width of the stream water surface and the non-vegetated channel was measured, and water depth was measured in the thalweg. Substrate composition was measured once, in February 1998, while widths and depths were measured on each sampling date (see below).

Particulate organic matter (POM) was sampled once, in July 1998, by installing perforated PVC pipes (300 mm long; 110 mm diameter; 9 mm diameter perforations) vertically into upwelling and downwelling zones in each of the upper and lower reaches respectively. Each of the POM samplers contained two flexible nylon mesh bags (≈ 10 mm mesh) filled with coarse gravel (7-17 mm diameter). The substrate-filled bags filled the POM samplers from 0-15 cm and 15-30 cm of their depth. Three POM samplers were dug into upwelling and downwelling zones in each of the upper and lower reaches, respectively (n = 18). Samplers were buried and closed with a removable perforated cap that was flush with the substratum. Samplers were installed in winter. After eight weeks, the substrate-filled bags were removed from the samplers, and POM was separated from gravel by elutriation. In the laboratory, invertebrates were removed and the mass of POM in each sample was determined following combustion at 400°C for five hours. POM is expressed as mg of ash free dry mass (AFDM) per litre of sediment. POM was not able to be determined seasonally, since several samplers were rendered inoperable by sediment scour or burial.

River discharge was determined on each sampling date (see below) as the product of cross-sectional area and mean velocity of a timed float over 10 metres (Gore, 1996).

Well Sampling

Samples were collected from wells in February (austral summer), May (autumn), August (winter), and November (spring), 1998. Stainless steel wells (15 mm internal diameter) were inserted to a depth of 0.3 m below the stream bed using a steel driving rod as described by Boulton et al. (1997). Ten wells were inserted at regular intervals along a 100 m reach of each river. Wells were inserted only where flowing surface water was present. In lower reaches, samples were taken about 5 metres upstream of the summer stream terminus. Immediately after insertion of each well, a hand-operated bilge pump was used to extract 5 litres of water and associated invertebrates, which were collected on a 63 μm

sieve. Invertebrates were preserved in 70% ethanol, to which Rose Bengal stain had been added to aid sorting of small individuals. All invertebrates were sorted under 15-35 x magnification and identified using the keys of Chapman & Lewis (1976) for Crustacea, Winterbourn et al. (2000) for Insecta and Cook (1983) for Acari.

During spring sampling, the turbidity of each sample was measured to give a relative measure of interstitial silt content. After the first litre of each sample had been withdrawn and passed through a 63 μm mesh sieve, a 200 ml sample of the filtered water was removed for turbidity measurement at 450 nm with a Hach spectrophotometer (Hach, 1990).

An indicative measure of hydraulic conductivity at sample sites was obtained by ranking the ease with which water samples could be drawn with the bilge pump. Wells that had low hydraulic conductivity took longer to withdraw 5 litres of sample (20-30 minutes per 5 litres), and were given a low ranking, whereas samples that were withdrawn as quickly as they could be pumped (< 1 minute per 5 litres) were ranked highest.

Hyporheic and surface water temperature and dissolved oxygen (DO) of water from each well were measured on each sampling occasion using a YSI DO meter. Hyporheic water was pumped in an unbroken stream until overflowing a small container. The DO probe was immediately inserted into this water and the temperature and DO recorded once readings had stabilised.

Potential hydraulic head, or vertical hydraulic gradient (VHG) was measured by inserting a transparent piezometer 30 cm into the streambed, utilizing the hole already made by the sampling well (sensu Boulton, 1993). The height of water in the piezometer was compared to surface water depth using a manometer (Boulton, 1993), and the height difference divided by the piezometer depth (30 cm). The resultant unitless ratio was positive in the presence of an upwelling zone and negative in a zone of downwelling stream water (Dahm & Valett, 1996).

Invertebrate Biomass

Animals were measured at 15-35x magnification using an eyepiece graticule in a dissecting microscope. Biomass was estimated from length using published power relationships for Amphipoda and Ceratopogonidae (Meyer, 1989); Copepoda (Pearre, 1980); Chironomidae, *Deleatidium* and Elmidae (Towers et al., 1994); and Polycentropodidae (Smock, 1980). For those taxa without published length-weight relationships, biovolume was estimated

from geometric shapes (Strayer & Likens, 1986). Nematodes, oligochaetes and syncarids were approximated to cylinders. Acari and Ostracoda were approximated to prolate spheroids, and isopods were measured as half-cylinders. Volume was converted to dry mass assuming a specific gravity of 1.05, and a wet-weight to dry-weight ratio of 0.15 (Strayer & Likens, 1986).

Biomass was determined for the 16 most abundant taxa, which accounted for 99% of total invertebrate abundance. Representatives of each taxon were chosen randomly, regardless of river, site or season to develop the length-biomass relationships. Sufficient individuals of each taxon were measured to achieve a ratio of standard error to mean biomass of less than 20% (Ramsay et al., 1997). From 10 (Syncaridae) to 30 (Elmidae) individuals were measured to obtain 20% precision. Invertebrate biomass of each sample was estimated by multiplying the mean biomass value for each taxon by the total number of individuals of that taxon in the sample (after Ramsay et al., 1997), and then summing for all taxa.

Invertebrates were assigned to predator or collector functional feeding groups using information in Chapman & Lewis (1976) for Crustacea and Acari; Winterbourn (2000) for Ephemeroptera, Trichoptera and Oligochaeta; Hilsenhoff (1991) for Coleoptera and Diptera; Pinder (1986) for Chironomidae; and Traunspurger (2000) for Nematoda.

Data analyses

Data were checked for normality and homogeneity of variances, and $\log_{10}$ or arcsine-transformed when necessary. To compare means of reach and seasonal variables, nested ANOVA was used; replicate samples were nested within reaches, and reaches nested within rivers (the source of "reach" replication). Season was not nested. All factors were fixed, and the error term for all factors was residual error (Zar, 1984). Scheffe post-hoc tests were used to identify differences between means. Kruskal-Wallis ANOVA was used to compare rank differences in hydraulic conductivity between seasons and reaches.

Relationships between invertebrate abundance and taxon richness and environmental variables were examined using correlation. Sequential Bonferroni adjustments of P-values were made (Rice, 1989) to minimise the likelihood of making type-I errors (rejecting a null hypothesis that is true), due to multiple hypothesis testing in a large correlation table.

Invertebrate community composition was compared among season, reach and river means using non-metric multidimensional scaling (MDS, Clarke, 1993) on PC-ORD (McCune & Mefford, 1999). Sorensen's index was used on $\log_{10}(x + 1)$ transformed total abundance data as the distance measure in the MDS ordinations (Faith et al., 1987). To help interpret the ordinations, axis scores were correlated (Spearman) with environmental variables and the abundance of common invertebrate taxa, and reported in text when significant (following adjustment of P-values using the sequential Bonferroni test).

Results

Environmental factors

Substrate composition was generally similar between rivers and reaches (Figure 2), with the modal particle size being 8–32 mm diameter. However, the Glentui River had a higher proportion (30 %) of sand and fine gravel (< 4 mm diameter) than the other rivers (≈ 10%). All rivers were of similar widths (4-9 m), depths (0.11-0.16 m), and had a mean discharge of 0.13-0.42 $m^3 s^{-1}$ (Table 1). River discharge was lowest in summer (0.02-0.17 $m^3 s^{-1}$) and highest in winter (0.27-0.71 $m^3 s^{-1}$).

AFDM of hyporheic sediments was low overall (mean = 45 mg per litre of sediment), and showed a weak decline with depth ($F = 4.6$, $P = 0.06$). Thus, mean AFDM was 62 mg per litre of sediment at 0-15 cm, and 28 mg per litre at 15-30 cm. AFDM did not differ between upper and lower reaches ($F = 0.92$, $P = 0.37$).

In the upper reaches, 43 % (52 out of 120) of samples were upwelling, compared to 14 % (17 out of 120) upwelling samples downstream. Lower reaches were also more strongly downwelling than upper reaches (Figure 3a), as indicated by the significantly more negative VHG overall ($F = 38.97$, $P < 0.0001$). VHG in upper reaches averaged – 0.05, and ranged from – 0.58 to + 0.08, while in lower reaches VHG averaged – 0.29, and ranged from – 1.17 to + 0.08. VHG did not vary significantly between seasons ($F = 0.05$, $P = 0.97$).

Hyporheic water temperature was 17-25 °C in summer and 2-8 °C in winter and did not differ between sampling reaches (Figure 3b). Hyporheic DO concentration was generally high (mean = 9.5 mg l^{-1}), and was 1-2 mg l^{-1} greater in lower reaches than upper reaches during summer and spring (Figure 3c). However, it was more similar between

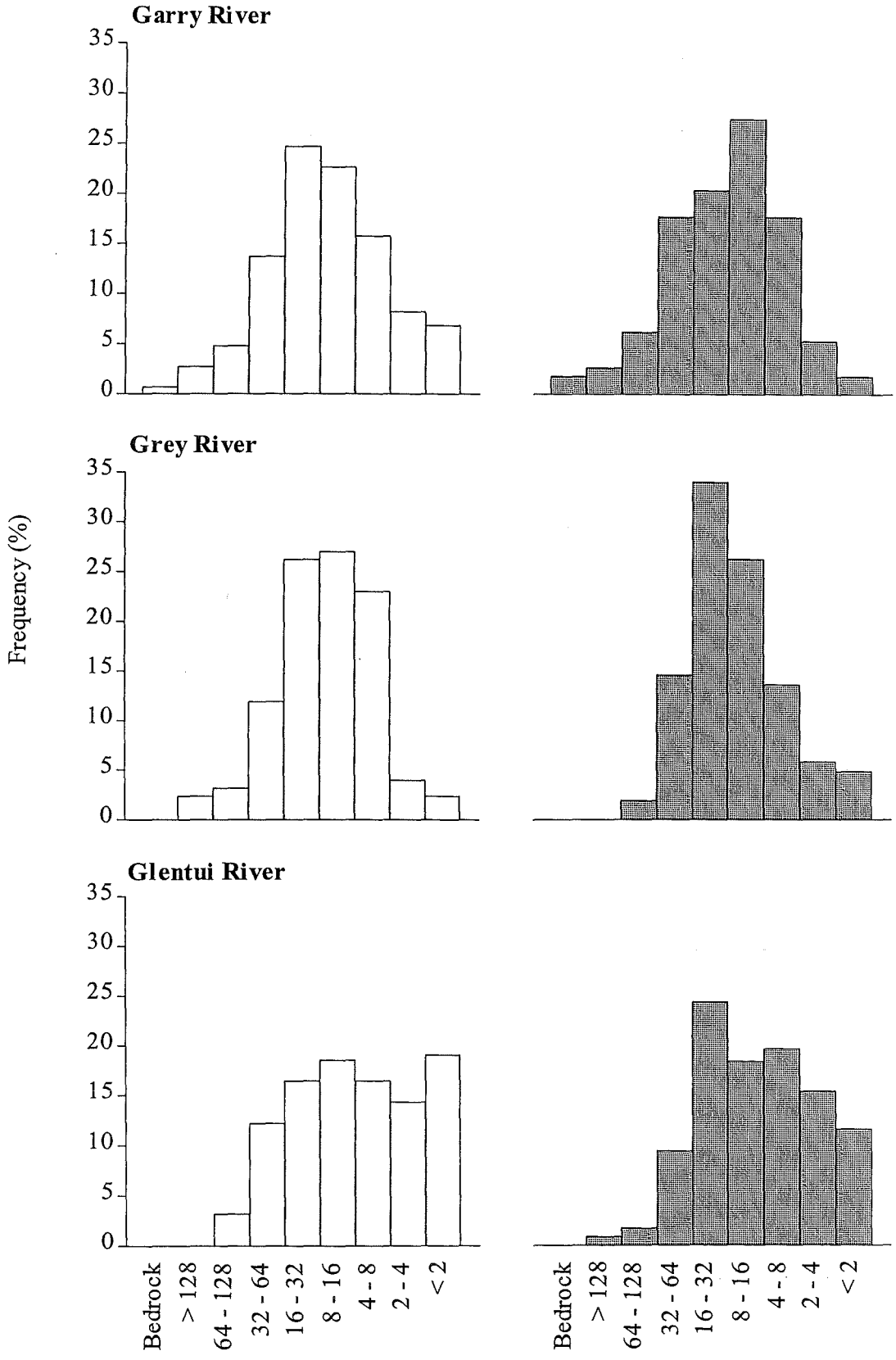

Figure 2. Particle size distributions of surface sediments from upper (*left*) and lower (*right*) reaches of the Garry, Grey and Glentui Rivers in February, 1998.

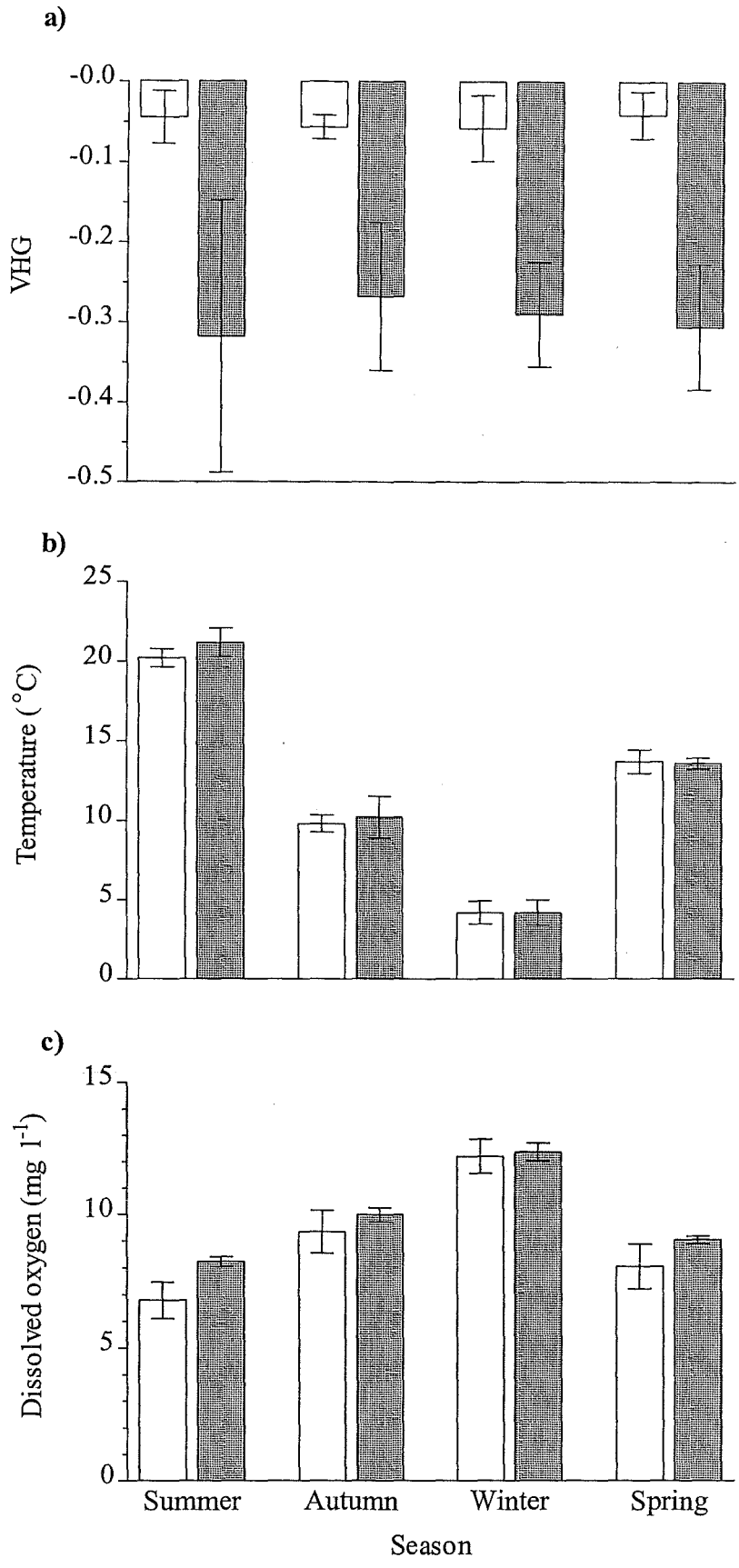

Figure 3. Mean (± 1 SE): a) VHG, b) hyporheic water temperature, and c) dissolved oxygen in upper (open bars) and lower (shaded bars) reaches of the three study streams in four seasons.

reaches in autumn and winter (ANOVA reach x season interaction, $F = 2.04$, $P < 0.05$). The difference between surface and hyporheic DO concentration was weakly and positively correlated with VHG (Table 2).

Mean turbidity of the first litre of water pumped was 2 750 NTU. Interstitial turbidity did not differ between reaches ($F = 1.9$, $P = 0.14$) and was highly variable within reaches (range = 200 – 8 930 NTU). Hydraulic conductivity varied with season (Kruskal-Wallis ANOVA, $P < 0.05$), and was greatest in winter and autumn when surface discharge was highest. Hydraulic conductivity and interstitial turbidity were negatively correlated (Table 2).

Invertebrates

A total of 32 311 invertebrates were collected from 240 samples in the four seasons. Non-insect taxa dominated the fauna numerically, and of these, harpacticoid copepods made up one third of the individuals. Water mites, oligochaetes and the amphipod *Paraleptamphopus subterraneus* were also very abundant (Table 3). An undescribed asellotan isopod, *Heterias* sp. (Janiridae), was less abundant, but still relatively common. This was the first New Zealand record of the genus, which occurs in South America, mainland Australia and Tasmania (G.D.F. Wilson, Australian Museum, pers. comm.).

Insects comprised 26 of the 47 taxa collected, but contributed only 15% of total invertebrate abundance. Insects were best represented by larval chironomids and a free-living polycentropodid caddisfly (Table 3).

On average, 135 individuals were taken per 5 litre pump sample, although density was greatest in lower reaches, and was influenced by season (Figure 4a). In summer and spring, mean invertebrate abundance was 195 individuals per 5 litres of water pumped in lower reaches, compared to 74 individuals per 5 litres in upper reaches. However, in autumn and winter the difference between reaches was significantly less (ANOVA $F = 3.3$, $P = 0.0008$), and mean abundance was 170 and 100 individuals per 5 litre sample in lower and upper reaches, respectively. Numerically dominant harpacticoids reached densities of up to 1013 individuals per 5 litres (in a sample from a lower reach in summer), and followed the same trend in abundance with reach and season as total invertebrate abundance (Figure 5a). Oligochaetes were also more abundant in lower reaches, but showed no consistent trend in abundance with season (Figure 5a).

Table 2. Correlation coefficients[1] for total invertebrate abundance, taxon richness and water quality parameters. Data include all seasons (n = 235), except for silt data, which are only from spring (n = 58). * = P < 0.05, ** = P < 0.01, *** = P < 0.001, following sequential Bonferroni adjustment (n = 35 comparisons).

	Hyporheic DO	DO difference	Temp.	Temp. difference	VHG	Silt	Hydraulic cond.
DO difference (surface-hyporheic)	−0.74***						
Hyporheic temperature	−0.79***	0.34***					
Temp. difference (surface-hyporheic)	−0.27***	0.03	0.25**				
VHG	−0.12	0.24*	0.07	0.04			
Silt	−0.18	0.07	0.01	0.31	0.07		
Hydraulic conductivity	0.04	0.01	−0.17	−0.02	0.10	−0.50**	
Abundance	0.24*	−0.35***	−0.04	−0.06	−0.05	−0.19	0.16
Taxon richness	0.54***	−0.37***	−0.57***	−0.19	0.03	−0.03	0.30***

[1] Pearson's correlation was used with all variables except hydraulic conductivity, for which Spearman rank correlation was used.

Table 3. Percentage abundance, biomass and functional feeding grouping of the most abundant hyporheic taxa collected from the Garry, Grey and Glentui Rivers during seasonal sampling in 1998. Insect taxa are marked with an asterisk.

Taxon		Abundance (%)	Biomass (%)	Functional feeding group
Harpacticoida	(Copepoda)	32.4	0.4	Collector
Acari		13.7	3.3	Predator
Oligochaeta		13.4	1.2	Collector
Paraleptamphopus subterraneus	(Amphipoda: Eusiridae)	10.9	26.4	Collector
Polycentropodidae*	(Trichoptera)	5.0	27.1	Predator
Nematoda		4.2	0.1	Collector
Cyclopoida	(Copepoda)	3.5	0.3	Collector
Ostracoda		2.9	0.9	Collector
Tanypodinae*	(Chironomidae)	2.8	13.0	Predator
Heterias sp.	(Isopoda: Janiridae)	2.4	3.1	Collector
Syncarida		1.9	0.2	Collector
Orthocladiinae	(Chironomidae)	1.9	8.8	Collector
Deleatidium sp.*	(Ephemeroptera: Leptophlebiidae)	1.2	3.4	Collector
Hydora sp.*	(Coleoptera: Elmidae)	1.0	6.4	Collector
Ceratopogonidae*	(Diptera)	1.0	1.6	Predator
Chironominae*	(Chironomidae)	0.6	2.6	Collector

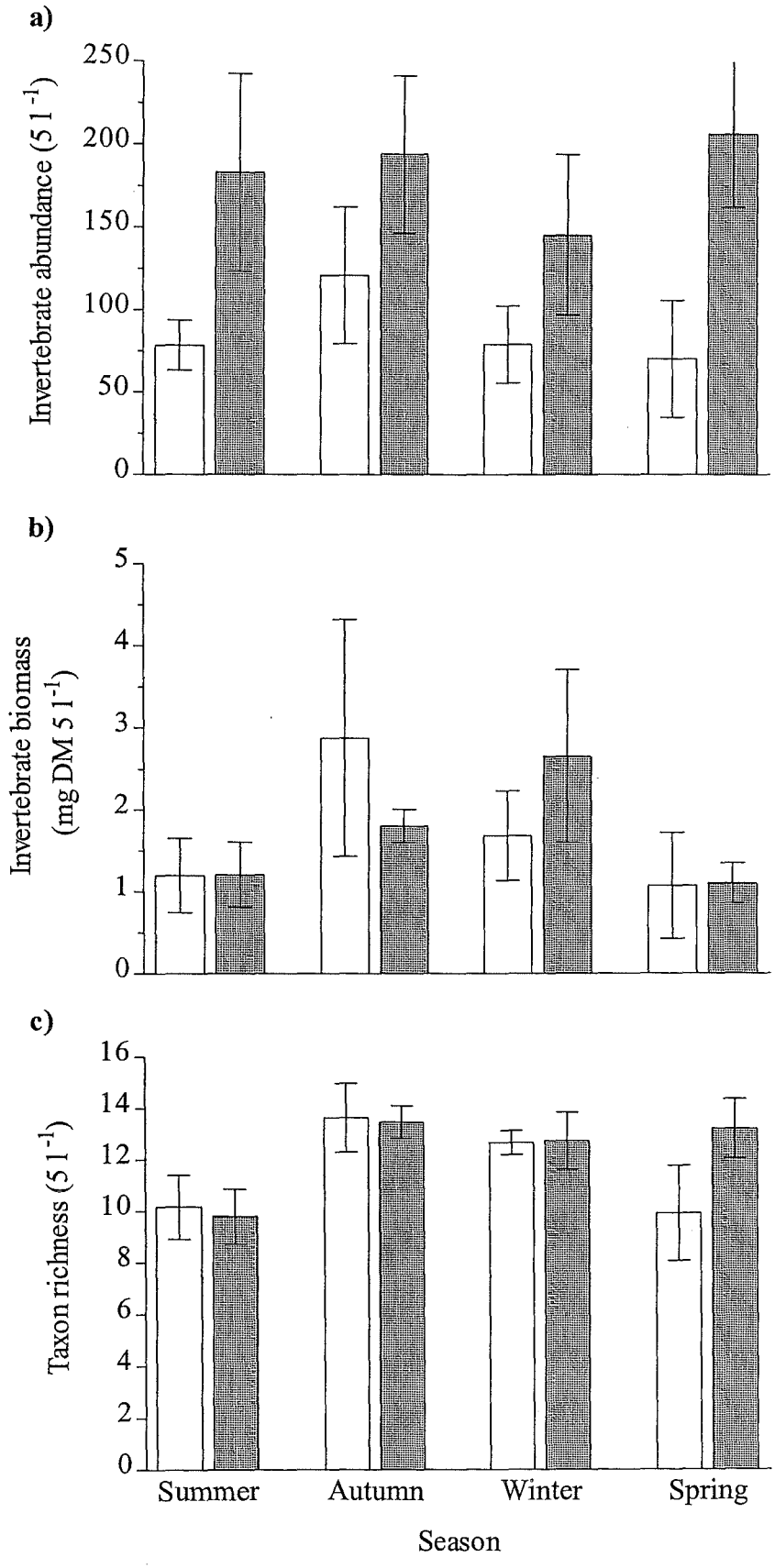

Figure 4: Mean (± 1 SE): a) faunal abundance, b) taxon richness, and c) faunal biomass in upper (open bars) and lower (shaded bars) reaches of the three study streams in four seasons.

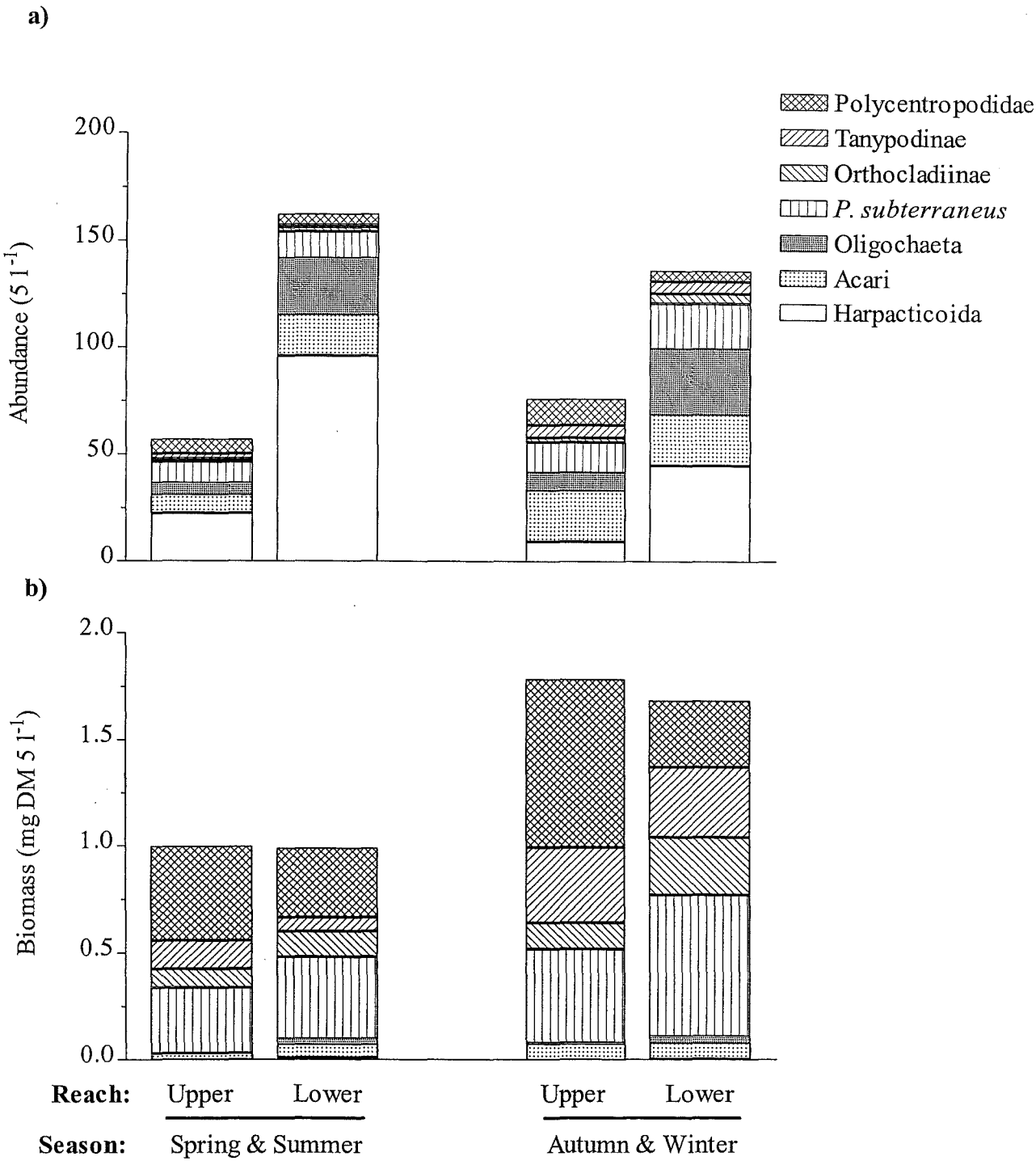

Figure 5. Mean a) abundance and b) biomass per sample of the six most abundant taxa taken from Ashley River tributaries in spring-summer and autumn-winter, and in upper and lower reaches.

Invertebrate biomass did not differ between reaches ($F = 1.4$, $P = 0.26$), but varied greatly with season ($F = 6.6$, $P = 0.0003$). Thus, mean invertebrate biomass was 1.2 mg dry mass per 5 litre sample in spring-summer, and nearly doubled to 2.25 mg per 5 litre sample in autumn-winter (Figure 4b). Greater biomass in autumn-winter was due, in particular, to the increased abundance of chironomids in the hyporheic zone at this time (Figure 5b). Mean chironomid biomass (including Tanypodinae, Chironominae and Orthocladiinae) increased from 0.22 mg dry mass per 5 litre sample in spring-summer to 0.65 mg per 5 litre sample in autumn-winter.

On average, 12 taxa were collected per 5 litres of water pumped (Figure 4c). Mean taxon richness was lowest during summer (mean = 10 taxa per sample) and greatest during autumn/winter (mean = 13 taxa per sample), ($F = 12.89$, $P<0.0001$; Figure 4c). Taxon richness was similar in upper and lower reaches in all seasons except spring, when upper sites had slightly fewer taxa (mean = 10 taxa per sample) than lower sites (mean = 13 taxa per sample; $F = 1.3$, $P = 0.04$). Non-insect taxa were more common than insects (means = 8 cf 3 taxa per sample), and followed the same seasonal and reach trends in richness as for total taxon richness. Insect taxon richness was also lowest in spring/summer (mean = 3 taxa per sample) and greatest in autumn/winter (mean = 5 taxa per sample) ($F = 6.22$, $P < 0.001$), but showed no variation between reaches ($F = 1.089$, $P = 0.37$).

The most abundant taxa contributed little to total biomass (Table 3, Figure 5). Thus, while harpacticoids comprised 32% of total abundance, they made up less than 0.5% of the total biomass. In contrast, amphipods, chironomids and a polycentropodid caddisfly made up about 80% of total measured biomass, but contributed only about 15% of total individuals. Percent invertebrate abundance and biomass were not correlated ($r_s = 0.05$, $P = 0.87$).

Predators, which included mites, polycentropodid caddisflies, tanypod chironomids and ceratopogonids (Table 3), made up 45 % of total invertebrate biomass, whereas collectors made up 55%. Mean predator biomass was 0.94 mg per 5 litres at upper sites and was significantly lower ($F = 5.5$, $P = 0.001$) at lower sites (mean = 0.59 mg per 5 litres). On average, predator biomass was 1.01 mg per 5 litres during autumn-winter and was significantly lower ($F = 14.0$, $P = 0.0002$) during spring-summer (mean = 0.52 mg per 5 litres). Collector biomass was also greater ($F = 9.73$, $P = 0.0001$) during autumn-winter (mean = 1.25 mg per 5 litres) than in spring-summer (mean = 0.62 mg per 5 litres), but did not differ between reaches ($F = 0.5$, $P = 0.64$).

Ordination of the invertebrate community yielded a two-dimensional solution with low stress (0.10), indicating a good relationship between the original dissimilarity matrix and distance in reduced 2-dimensional ordination space (Clarke, 1993). Samples taken in autumn and winter tended to be higher on Axis 2 than summer and spring samples (Figure 6a). In addition, samples from lower reaches tended toward the left of axis 1, while upper reach samples tended toward the right (Figure 6b). Invertebrate composition differed little between the different rivers sampled (Figure 6c). Harpacticoid abundance was negatively correlated with axis 1 scores (r_s = -0.74, P = 0.001), as was the abundance of oligochaetes (r_s = -0.65, P = 0.002). Axis 2 scores were negatively correlated with temperature (r_s = -0.71, P = 0.004) and harpacticoid abundance (r_s = -0.82, P < 0.0001). Axis 2 scores were positively correlated with the proportion of total abundance made up by insects (r_s = 0.78, P = 0.0004) and with elmid abundance (r_s = 0.69, P = 0.007).

Associations between invertebrate communities and environmental factors

Invertebrate abundance and taxon richness were significantly and positively correlated with DO concentration and the difference between surface and hyporheic DO (Table 2). Taxon richness was also correlated negatively with temperature, and positively correlated with hydraulic conductivity (Table 2).

As DO and temperature were correlated in the full data set (Table 2), and both varied with season (Figure 3), further correlations were calculated between DO and abundance for each season and reach (Figure 7). These indicated that the association between DO and abundance was stronger at upper sites (r = 0.39 – 0.68), which generally had a wider range of DO concentrations. In contrast, lower sites generally had high DO concentrations, which were weakly associated with abundance (r = 0.06 – 0.25). Correlations between DO and abundance at upper sites were strongest in spring (r = 0.58) and summer (r = 0.68) and weakest in autumn (r = 0.39) and winter (r = 0.49).

Most taxa were found in samples with high DO concentrations (means = 9.2 – 10.8 mg l^{-1}), however 10 of the 16 most abundant taxa (mainly non-insects) were taken from wells with DO concentrations < 3 mg l^{-1} (Table 4). A single well with a DO concentration of 2.1 mg l^{-1} contained 7 invertebrate taxa and no insect taxa. In addition, most individuals were found where the water was cool (means = 7.9 – 13.4 °C), but all taxa were found at temperatures above 22 °C, and 5 taxa were found at 25.0 – 25.5 °C (Table 4).

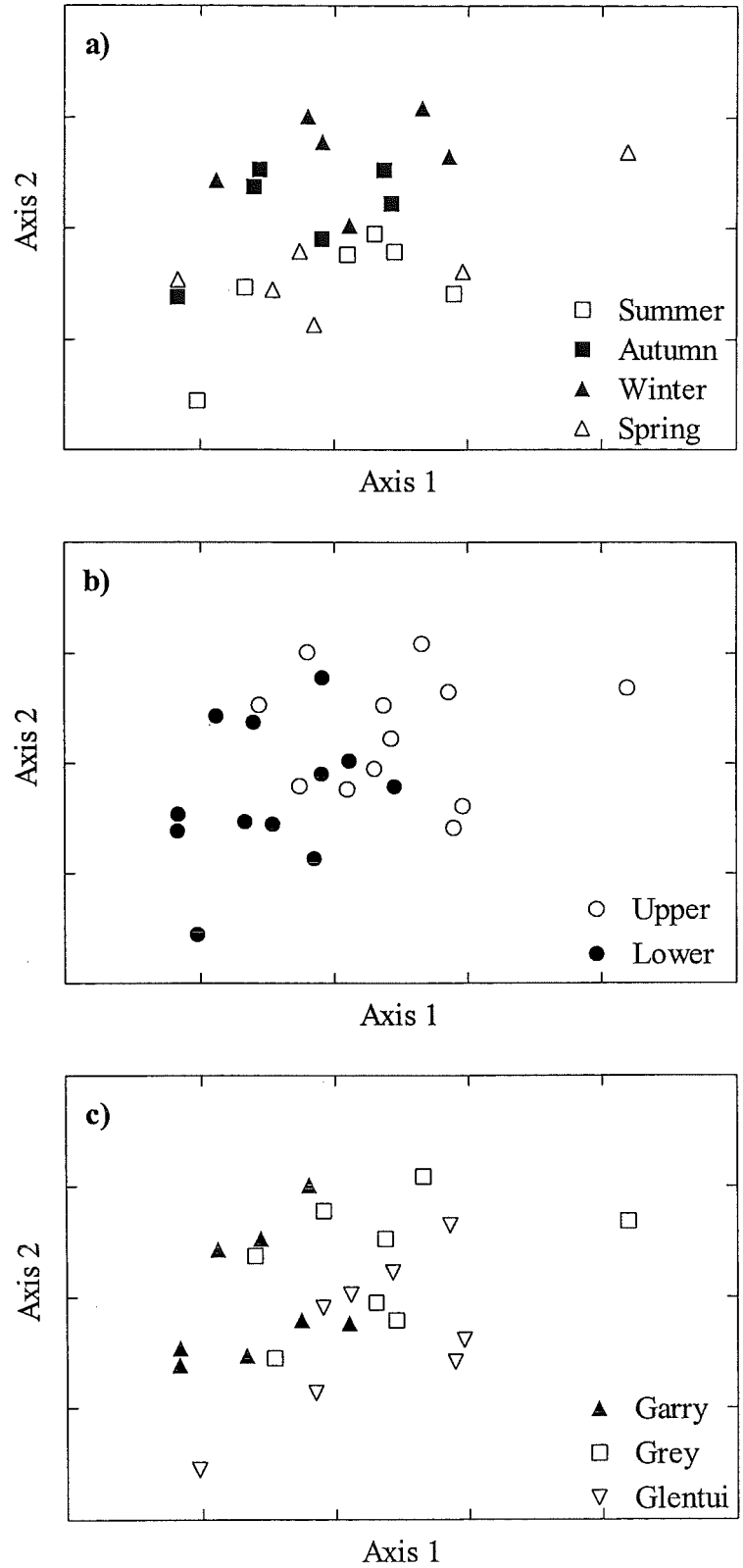

Figure 6. MDS ordinations (stress = 0.10) of invertebrate assemblages from the Ashley River tributaries, showing axis scores for each a) season, b) reach, and c) river.

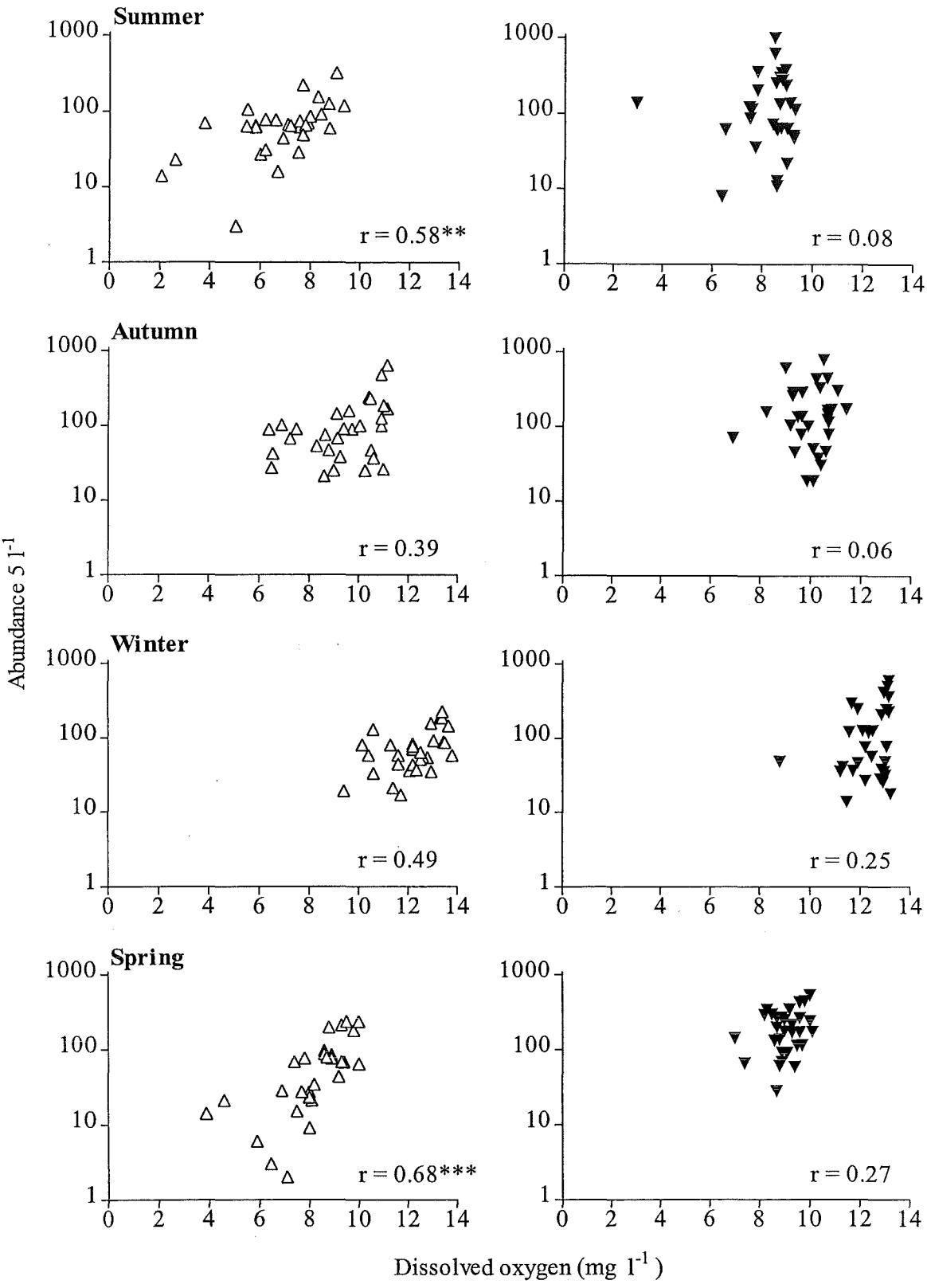

Figure 7. Relationships between dissolved oxygen concentration and invertebrate abundance (log scale) in samples taken from Ashley River tributaries in upper (*left*) and lower (*right*) reaches in four seasons. Correlation coefficients (r) are shown; ** = $P < 0.01$, *** = $P < 0.001$, following sequential Bonferroni adjustments (n = 8 comparisons).

Table 4. Means and ranges of dissolved oxygen and water temperature in hyporheic wells from which the most abundant taxa were recorded in the Garry, Grey and Glentui Rivers. n = number of samples in which each taxon was present. Numbers in brackets are values for all samples.

Taxon	Dissolved Oxygen ($mg\ l^{-1}$)		Temperature (°C)		n
	Mean	Range	Mean	Range	
	(9.5)	(2.1 – 13.8)	(12.2)	(1.6 – 25.4)	(239)
Hydora sp.	10.8	6.0 – 13.8	7.9	1.6 – 22.3	70
Ceratopogonidae	10.3	3.9 – 13.5	9.2	1.9 – 22.3	96
Tanypodinae	10.2	2.9 – 13.8	10.1	1.6 – 24.3	132
Deleatidium sp.	10.2	5.9 – 13.5	11.4	1.6 – 25.4	90
Chironominae	10.2	7.0 – 13.5	10.9	1.6 – 23.5	40
Ostracoda	9.8	5.5 – 13.8	11.5	1.6 – 24.3	117
Heterias sp.	9.8	2.1 – 13.8	12.0	1.6 – 24.3	123
Acari	9.7	2.1 – 13.8	11.7	1.6 – 25.1	218
Polycentropodidae	9.7	2.7 – 13.8	11.9	1.6 – 24.3	170
Syncarida	9.7	3.9 – 13.8	12.4	1.6 – 25.1	113
Oligochaeta	9.5	2.1 – 13.8	12.1	1.6 – 25.4	215
P. subterraneus	9.5	2.1 – 13.8	11.8	1.6 – 24.3	191
Nematoda	9.5	2.1 – 13.8	12.2	1.7 – 24.3	162
Orthocladiinae	9.5	2.7 – 13.7	12.2	1.9 – 25.4	150
Harpacticoida	9.4	2.1 – 13.7	12.5	1.6 – 25.4	219
Cyclopoida	9.2	2.1 – 13.4	13.4	2.0 – 25.4	166

Discussion

Hydrologic factors affecting the hyporheos

Upstream reaches of rivers draining the Canterbury foothills contained both upwelling and downwelling zones, while downstream, intermittent reaches were dominated by strong downwellings. VHG ranged from +0.08 to –1.16; a wide range compared to that reported by Brunke & Gonser (1999) in the Töss River, Switzerland (+ 0.08 to – 0.12) or by Hendricks & White (1995) in Maple River, USA (+0.18 to –0.08). Downwellings of the magnitude measured in this study are more comparable to those reported in intermittent desert streams in North America (Valett et al., 1990) and Australia (Cooling & Boulton, 1993). For example, Valett (1993) found the VHG in Sycamore Creek, Arizona, varied from + 0.29 upstream, to – 0.89 downstream, where flow was intermittent.

Intermittency of flow in lower reaches during summer may have influenced differences in invertebrate community composition among reaches. Although samples were taken upstream of the dry stream terminus, the terminus retreated several metres upstream during the course of the day, leaving wells dry (to > 40 cm depth) where there had been surface flow present only a few hours before. Harpacticoid copepods numerically dominated the fauna of lower reaches, and they were most abundant during summer. Copepods have short generation times (1-3 weeks from egg to adult) during warm periods, and many taxa have eggs that are resistant to desiccation (Williamson, 1991; Dole-Olivier et al., 2000). It therefore seems likely that harpacticoids proliferated in downwelling reaches due to their tolerance of intermittent flow, and high reproductive output at elevated summer temperatures.

The greater prevalence of upwellings in upper reaches resulted in lower hyporheic DO concentrations than in predominantly downwelling reaches. Lower DO concentrations in upper reaches were associated with a negative association between DO and invertebrate abundance, and lower overall invertebrate abundance, than in downwelling reaches. While invertebrates were more abundant at high DO concentrations, 10 of the 17 most abundant taxa tolerated hypoxic conditions (DO concentration < 3 mg l^{-1}). Nevertheless, insect taxa were typically found at higher DO concentrations and were not found below 2.5 mg l^{-1}. In a survey of several Sonoran Desert streams, Boulton et al. (1992) found most common hyporheic taxa tolerated DO concentrations < 1.5 mg l^{-1}, and all were found at mean DO concentrations of 3 – 4 mg l^{-1}. Data from the Sonoran Desert streams may indicate a

greater tolerance to hypoxia than in the Canterbury rivers. However, DO concentration always exceeded 2 mg l^{-1} in the Canterbury rivers and experimental work may show that elements of the New Zealand hyporheic fauna have greater tolerance of low DO than indicated by this survey.

Seasonal factors affecting the hyporheos

Insect abundance was greatest in the hyporheic zone of the Canterbury rivers in autumn and winter. As insects were generally larger than non-insect taxa such as harpacticoids and oligochaetes, their increase in autumn and winter resulted in a peak in invertebrate biomass at this time. Increased insect abundance in autumn-winter in the hyporheos has been noted by others (e.g., Williams & Hynes, 1974; Poole & Stewart, 1976; Strommer & Smock, 1989; Marchant, 1995; Adkins, 1997; Fraser & Williams, 1998) and is most likely caused by the hatching of larvae from eggs laid in summer (Williams & Hynes, 1974). As the abundance of insects in the hyporheic zone is greatest at a time when stream discharge is also greatest, several authors have suggested that the hyporheic zone may serve as a refuge from scouring floods (Poole & Stewart, 1976; Williams & Hynes, 1976; Marchant, 1995). However, field experiments have shown that invertebrates do not migrate vertically into the substrate in response to artificially increased stream flow, and that colonisation of surface substrata by invertebrates is achieved more by drift than by upward movement from the hyporheic zone (Palmer et al., 1992; Gayraud et al., 2000). In the Canterbury rivers, my data also indicate a passive accumulation of insects in the hyporheic zone, rather than migration to avoid flood disturbance, as sampling was done during a dry year with no large floods.

On average, predators contributed about 45% of total invertebrate biomass, and were most abundant in autumn and winter. The commonest predators were polycentropodid caddisflies and tanypod chironomids. Polycentropodids and tanypods have also been collected from the hyporheic zone of two Otago streams (Scarsbrook, 1995) and several streams near Cass (Adkins, 1997). Tanypods feed non-selectively on a variety of interstitial fauna (Schmid & Schmid-Araya, 1997), while polycentropodids are net-spinning predators that may also ingest detritus, and whose prey is known to include chironomids, mayflies and oligochaetes (Winterbourn, 2000). The role of predation in hyporheic communities is poorly understood (Schmid & Schmid-Araya, 1997; Boulton, 2000; Hakenkamp & Morin, 2000; Hakenkamp & Palmer, 2000), however, their large

contribution to total biomass in this study suggests that predation pressure may be high in the hyporheic zone.

Integrating seasonal and hydrologic effects on the hyporheos

Differences between seasons were reflected in the hyporheic zone by changes in water temperature and hydrology. Increased river flow during autumn and winter reduced the hyporheic residence time of water and resulted in less difference in DO concentration between upwelling and downwelling zones. Furthermore, DO levels were high overall. Stanley & Boulton (1995) also found that differences in DO concentration between upwelling and downwelling zones of Sycamore Creek were greatest when stream discharge was lowest, and least following floods.

Increased stream discharge affected the relationship between DO concentration and invertebrate abundance differently in upper and lower reaches. In upper reaches, upwellings resulted in patches of the hyporheic zone that were low in DO during summer and spring. In winter and autumn, when flow was high, VHG did not change, but DO was high due to increased flow, and the effect of upwellings on DO and the hyporheos were reduced. In contrast, as lower reaches were predominantly downwelling regardless of season, the hyporheic zone was well oxygenated throughout the year.

VHG and stream discharge interacted to influence total invertebrate abundance, but did not appear to affect the taxonomic composition of the hyporheos. Thus, harpacticoids were most abundant in downwelling reaches and in summer, but differences in their abundance between reaches did not vary with season. In addition, insects were most abundant during autumn and winter, regardless of reach differences in hydrology. Therefore, reach differences in vertical hydrologic exchange were reflected in community composition, and differences in faunal composition between reaches persisted throughout the year. Boulton & Stanley (1995) also found that the composition of the invertebrate fauna in upwellings and downwellings persisted through time in the hyporheic zone of Sycamore Creek, although flooding and drying changed community composition significantly.

Data from this chapter indicate that changes in VHG and season influence the abundance and composition of the hyporheos. Oxygen appeared to be the primary environmental factor affected seasonally by VHG. However, other factors such as fine sediment deposition (Boulton, 1993; Brunke, 1999; Boulton & Quinn, 2000), POM content

(Brunke & Gonser, 1999), and nutrient availability (Stanley & Boulton, 1995; Valett et al., 1996; Dent et al., 2001) may also be affected by VHG. In a survey of the hyporheos of 14 North American streams, Strayer et al. (1997) found positive associations between invertebrate abundance, sediment grain size and organic matter content when oxygen concentration exceeded 1 mg l^{-1}. The data presented by Strayer et al. (1997) suggest that a hierarchy of environmental factors limit the distribution and abundance of the hyporheos. In the Canterbury rivers, the wide range of invertebrate abundance found in downwelling reaches also suggests that other factors limit abundance when DO concentration is not limiting.

In summary, the importance of vertical hydrologic exchange in structuring the hyporheic communities of three Canterbury rivers was dependent on seasonal factors and reach characteristics (Figure 7). In upland, or constrained valley reaches, upwelling conditions resulted in seasonal reductions in DO that may have affected the biota. Lowland or unconstrained valley reaches were less influenced by upwelling conditions and DO, but other environmental factors such as organic carbon supply or substrate composition may be more important determinants of invertebrate composition in these settings.

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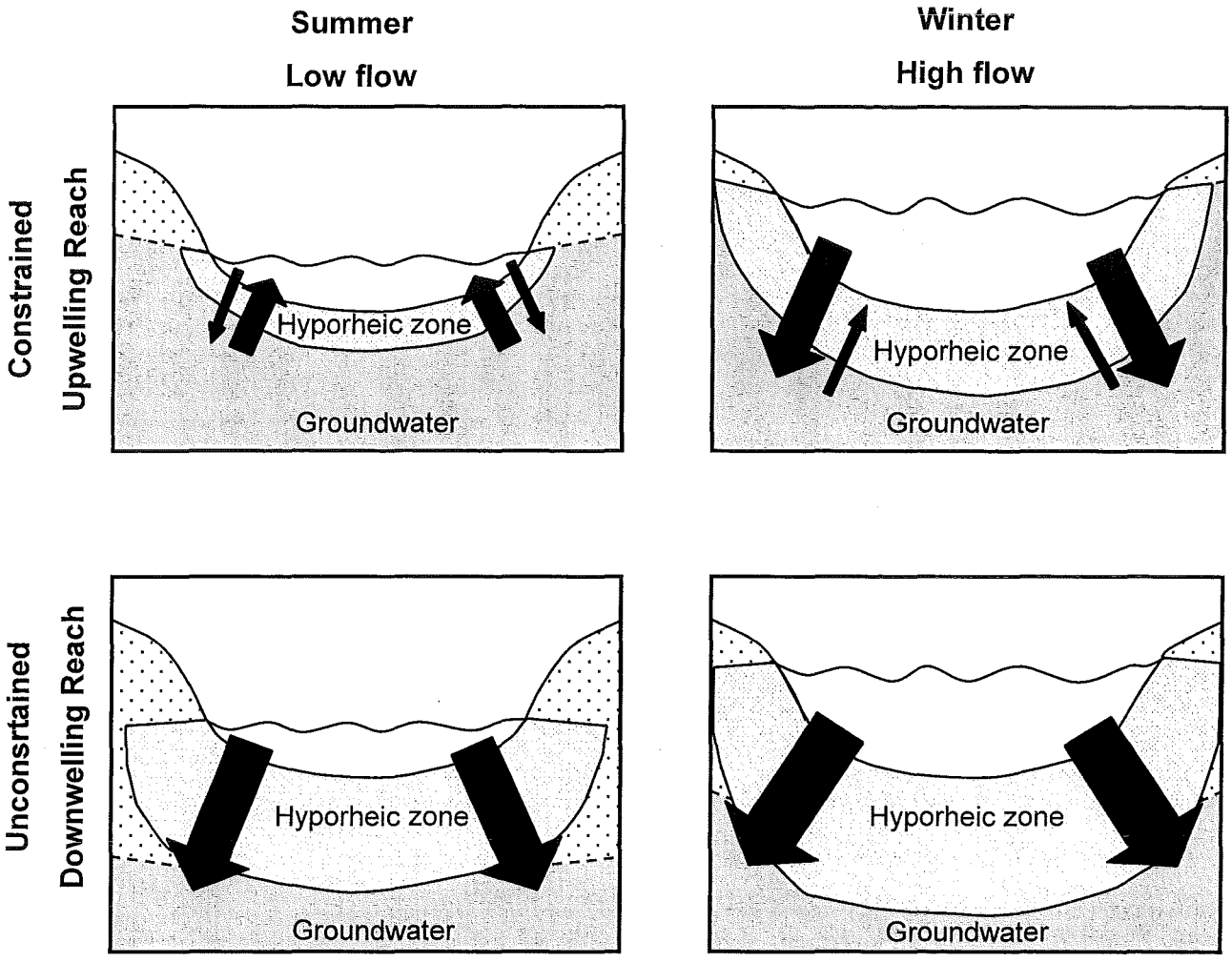

Figure 8. The influence of (seasonal) changes in surface water flow on vertical hydrologic exchange through the hyporheic zone in stream channels with different geomorphology. Upper panels represent stream reaches influenced by both upwelling and downwelling water, while the lower panels show reaches dominated by downwelling hydrologic conditions. Arrows indicate direction of the vertical hydraulic gradient (VHG), and arrow widths indicate the relative effect of VHG on the biota.

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Chapter 3

Factors influencing hyporheic invertebrate communities and community respiration in a temperate lowland river

Introduction

Contemporary models of river ecosystems stress the importance of linkages between surface, subsurface and terrestrial components of the landscape in the functioning of hyporheic communities (Vervier et al., 1992; Stanford & Ward, 1993). The hyporheic zone is essentially a 'middle zone' (sensu White, 1993) between channel and groundwaters, where a mixing of waters containing different quantities and kinds of solutes, organic matter and biota occurs. Indeed, Boulton (2000) considered groundwater-surface water ecotones worthy of 'frontier' status, due to their dynamic nature.

Central to the functioning of the hyporheic zone is its ability to transport water between surface and subsurface regions of a river and its floodplain. The permeability, or hydraulic conductivity, of bed material is expected to limit the flux of material in the hyporheic zone, while the direction of hydrologic exchange between surface and subsurface waters further limits the processes and biota that may occur there (Brunke & Gonser, 1997). Long hyporheic residence times, and upwelling subsurface waters both bring about poorly-oxygenated interstitial water, and are expected to result in a distinctive, less diverse fauna than in downwellings or locations where hydraulic conductivity is higher (Brunke & Gonser, 1997). Surprisingly, how permeability and the direction of hydrologic exchange interact to affect hyporheic communities has not been studied.

A major obstacle to the advancement of an understanding of hyporheic ecology is methodological (Palmer, 1993); physically reaching the hyporheic zone is very difficult, particularly in coarse sediments, large rivers, or when trying to penetrate deep into the stream bed. For these reasons, the majority of hyporheic research has focussed on small upland streams (e.g., Williams & Hynes, 1974; Marchant, 1988; Pusch & Schwoerbel, 1994), or those with sandy substrates (e.g., Boulton & Stanley, 1995; although see Stanford & Gaufin, 1974; Marmonier et al., 1995). This has led to a paucity of information

on the ecology of the hyporheos in lowland settings, where the hydrology and biology is likely to be quite different. In addition to natural longitudinal change (Vannote et al., 1980), human influences such as flow regulation or flow depletion are likely to have a greater impact on the lower reaches of rivers, where there is little flow compensation by groundwater exfiltration (White, 1993).

As well as differences in the type of river studied, different sampling methods yield data that do not facilitate cross-comparisons between studies. Differences in sampling bias between methods have been observed in wetland research (Turner & Trexler, 1997), as well as in streams (Fraser & Williams, 1997), where it has been suggested that a variety of methods should be used, in order to completely sample the biota.

In order to adopt a functional view of the hyporheic zone as a filter between river, groundwater and the land, both microbial and metazoan ecology needs to be considered. Both microbial activity and invertebrate abundance may decline with depth within the substrate, and they have been related to the depth distribution and abundance of organic matter (Pusch, 1996). However, Rounick & Winterbourn (1983) found that buried leaves (10 cm depth) were colonised by the same invertebrate fauna as those at the substrate surface, despite lower microbial respiration on buried leaves. This suggests that different components of stream communities need not respond in similar ways to depth and resource availability.

The Canterbury Plains are traversed by a large number of alluvial rivers. Despite the great potential for an active hyporheic zone in these rivers, no studies of their hyporheic fauna or microbial activity have been published. Driven by this lack of biological information concerning surface-subsurface biological interactions in lowland rivers in general, and in New Zealand in particular, the aims of my study were to:

a) compare site and seasonal differences in invertebrate composition of a lowland river and relate them to physicochemistry;
b) compare between-reach and depth distributions of community respiration and relate them to physicochemistry; and
c) compare the fauna sampled by pumping and colonisation pots.

Methods

Study sites

The Waipara River, in North Canterbury, has a catchment area of approximately 740 km^2, and includes foothills, plains and some coastal ranges (Canterbury Regional Council, 1993). Catchment vegetation is primarily improved pasture with scattered patches of forest in the foothills and coastal ranges. In recent years numerous vineyards have also been established in the middle reaches of the catchment. Willows (*Salix* spp.), scrub and grasses dominate the riparian zone. My study focussed on the lower reaches of the river, which have a low gradient (mean $\approx$ 0.5%) and are sparsely vegetated. Water level data from groundwater bores in the area indicate that the influence of the Waipara River on local groundwater is mostly limited to recent (Holocene) fluvioglacial deposits within 1-2 km of the river and to depths <20 m (Loris, 2000). Eight sampling localities were selected along lower reaches of the river. Sites were numbered from one to eight in order from downstream (near the river mouth) to upstream (Figure 1). The most upstream site was approximately 38 km from the coast and 180 m above mean sea level. Sites 3-5 and 8 were located in incised, or constrained valley reaches (lateral extent of recent alluvium ca 50-300 m wide), whereas the remaining sites were in relatively unconstrained reaches (ca 700-1300 m wide). All reaches were dominated by fine to coarse alluvial gravel (16 – 56 mm diameter) and were broad and shallow (Table 1). The section of river studied was predominantly 'run' habitat (Jowett, 1993), with riffles and especially pools being relatively uncommon. For this reason, only run habitat was sampled.

River discharge is gauged continuously between Sites 7 and 8 (Figure 1) where mean annual flow is 2.5 $m^3 s^{-1}$ (Canterbury Regional Council, 1996). Multiple gaugings along the Waipara suggest that the river gains flow from tributaries, springs and shallow groundwater between Sites 2 and 8. Downstream of Site 2 flow is lost (Table 1), either naturally to shallow groundwater, or artificially through abstraction for irrigation. Many farms use groundwater from the Waipara area for irrigation, and the demand for this water has increased greatly in recent years due to subdivision for 'lifestyle' blocks (Loris, 2000).

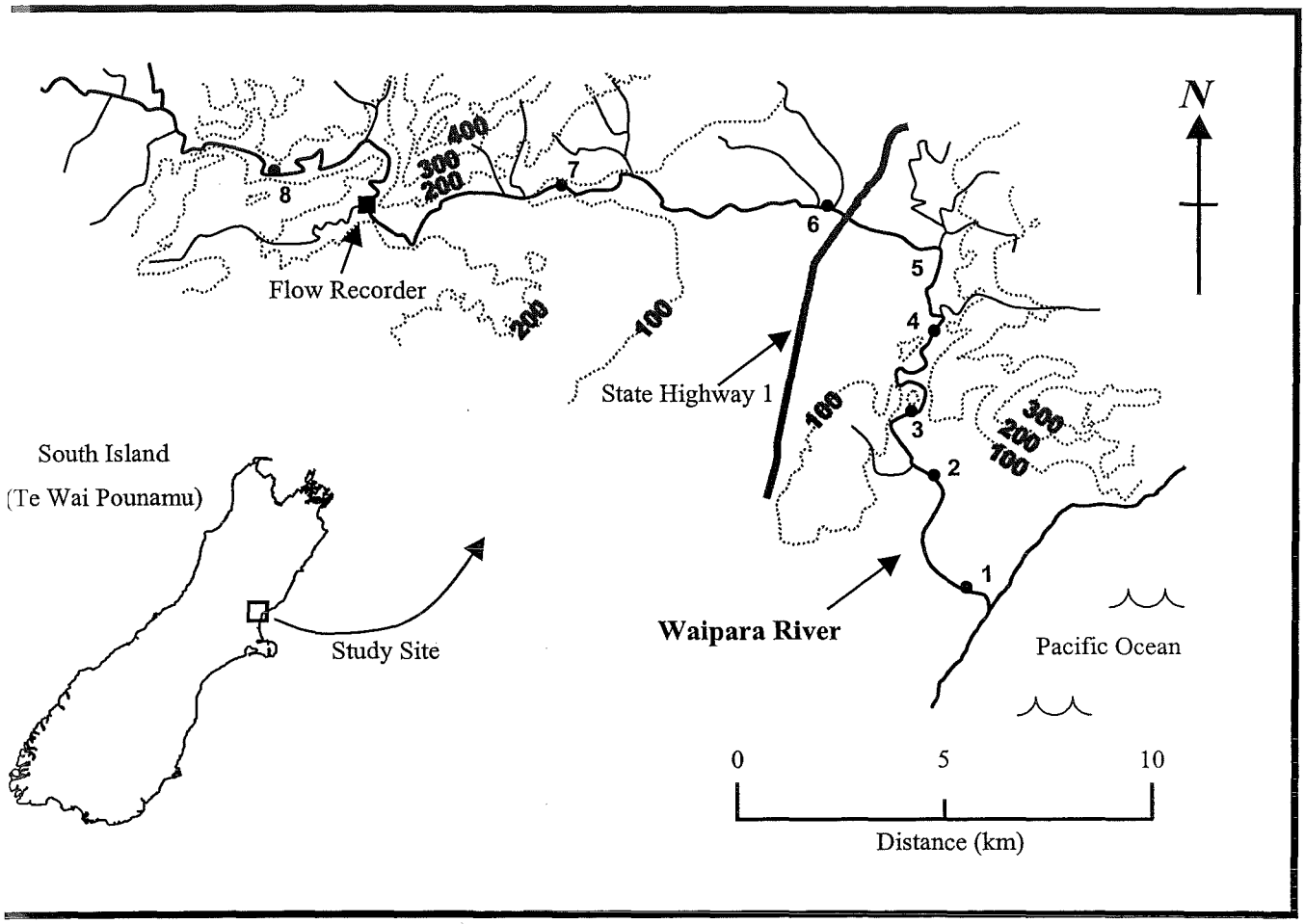

Figure 1. Location of study sites (numbered) along the Waipara River. Dashed grey lines show 100 m elevation contours.

Table 1. Characteristics of eight study sites on the Waipara River measured in December 1998. Values are means (n = 3), except 'd50', which is median particle diameter (n ≈ 100).

Site	Width (m)	Depth (m)	Flow (m^3 s^{-1})	d50 (mm)
1	19.6	0.17	1.59	20
2	11.1	0.31	2.06	39
3	12.0	0.32	1.99	16
4	12.7	0.25	2.06	29
5	8.7	0.36	1.49	17
6	13.5	0.22	1.35	28
7	15.0	0.29	1.17	27
8	7.5	0.24	1.00	56

Pump-sampling

Open-ended, stainless steel wells (15 mm internal diameter) were inserted to a depth of 0.3 m below the stream bed using a steel driving rod as described by Boulton et al. (1997). Five wells were inserted in a run, at the head of a riffle, in each of the eight reaches. Each reach was about 10 m long and wells were spaced diagonally across the wetted channel width over this distance. Pump-sampling began immediately after well insertion. A hand-operated bilge pump was used to extract 5 litres of water and associated invertebrates, which were caught on a 63 μm sieve. Invertebrates were preserved in 70% ethanol, to which Rose Bengal stain had been added to aid sorting of small individuals. All invertebrates were sorted under 15-35 x magnification and identified using the keys of Chapman & Lewis (1976) for Crustacea, Winterbourn et al. (2000) for Insecta and Cook (1983) for Acari. Samples were collected in September (austral spring) and December (summer) 1998, and March (autumn) and June (winter) 1999.

After the first litre of each sample had been withdrawn and passed through a 63 μm mesh sieve, a 200 ml sample of the filtered water was removed for turbidity measurement at 450 nm with a Hach spectrophotometer (Hach, 1990). To assess the suitability of turbidity as a measure of suspended sediment, the amount of silt and clay in December samples was quantified in the laboratory using pipette analysis (Folk, 1965).

Hyporheic and surface water temperature, and dissolved oxygen (DO) of water from each well were measured on each sampling occasion using a YSI DO meter. This was done following invertebrate sampling by pumping water in an unbroken stream until a small container overflowed. A DO probe was then inserted and the temperature and DO recorded once readings had stabilized.

Potential hydraulic head, or vertical hydraulic gradient (VHG) was measured by inserting a transparent piezometer 0.3m into the streambed, utilizing the hole already made by the sampling well (sensu Boulton, 1993). The height of water in the piezometer was compared to surface water depth with a manometer, as described by Boulton (1993). A positive head indicated the presence of an upwelling zone, while a negative head indicated a zone of downwelling stream water. Water depth and velocity (at 0.4 x depth) were measured adjacent to each sampling well using a metric rule and Marsh-McBurney current meter, respectively.

Streambed permeability was assessed at each site with a Terhune standpipe (Terhune, 1958) driven 0.3m into the streambed at each well sampling location. Interstitial

flow rates were determined at each site by measuring the amount of water that could be withdrawn from the standpipe over a given period of time (10-60 seconds, depending on hydraulic conductivity). Flow rates (ml $minute^{-1}$) were converted to permeability values (cm $minute^{-1}$), using the rating curve of Terhune (1958). Permeability was measured in September and December only due to breakages of the standpipe.

Colonisation Pots

Colonisation pots consisted of two pieces: an outer sleeve and an inner, removable basket. The outer sleeve comprised a frame made from a 450 mm long section of 110 mm diameter PVC pipe, with nine large windows cut into the sides (Figure 2). Stiff plastic mesh (8 mm mesh opening) was attached to the outside of the frame using plastic cable ties. An end cap was glued to the bottom end of the sleeve, and the top was left open. The removable basket consisted of a cylinder of the same plastic mesh used on the sleeve, rolled to a diameter slightly smaller than that of the outer sleeve, so that it fitted snugly inside the outer sleeve. The bottom end of the mesh cylinder was attached with plastic cable ties to the outside of a PVC end-cap. The overlapping edges of the mesh basket were kept together by lacing nylon line through the mesh, along the length of the cylinder. The mesh baskets were filled with 7-17 mm gravel, collected from a local alluvial quarry. The substrate-filled baskets were slid into the outer sleeves, and transported to each site.

To insert each pot into the river bed, a steel cylinder (50 cm diameter) was held on the streambed, while a hole was dug inside. The cylinder prevented the excavated hole from becoming too large due to the erosive action of the water current. Excavated sediment was kept in a large bucket until after the colonisation pot had been placed in the hole, with its top flush with the substrate surface. Excavated substrate was then poured back around the pot, and the steel cylinder was removed.

Five sets of colonisation pots were dug in at Sites 1, 3, 4, 5, and 8 at the end of February 1999. Site 1 had no surface flow at the time of pot emplacement, but received intermittent flow during the 6-week colonisation period. After six weeks, the inner substrate-filled basket was withdrawn from the stream, the nylon lacing was removed, and the substrate was divided into three depth sections of approximately 0-15 cm, 15-30 cm and 30-45 cm depth and placed in clean plastic containers. Each sediment sample was kept cool (ca 5°C) in the dark, and brought back to the laboratory for respiration measurements within 6 hours. After the colonised substrate had been removed, the sides of the mesh

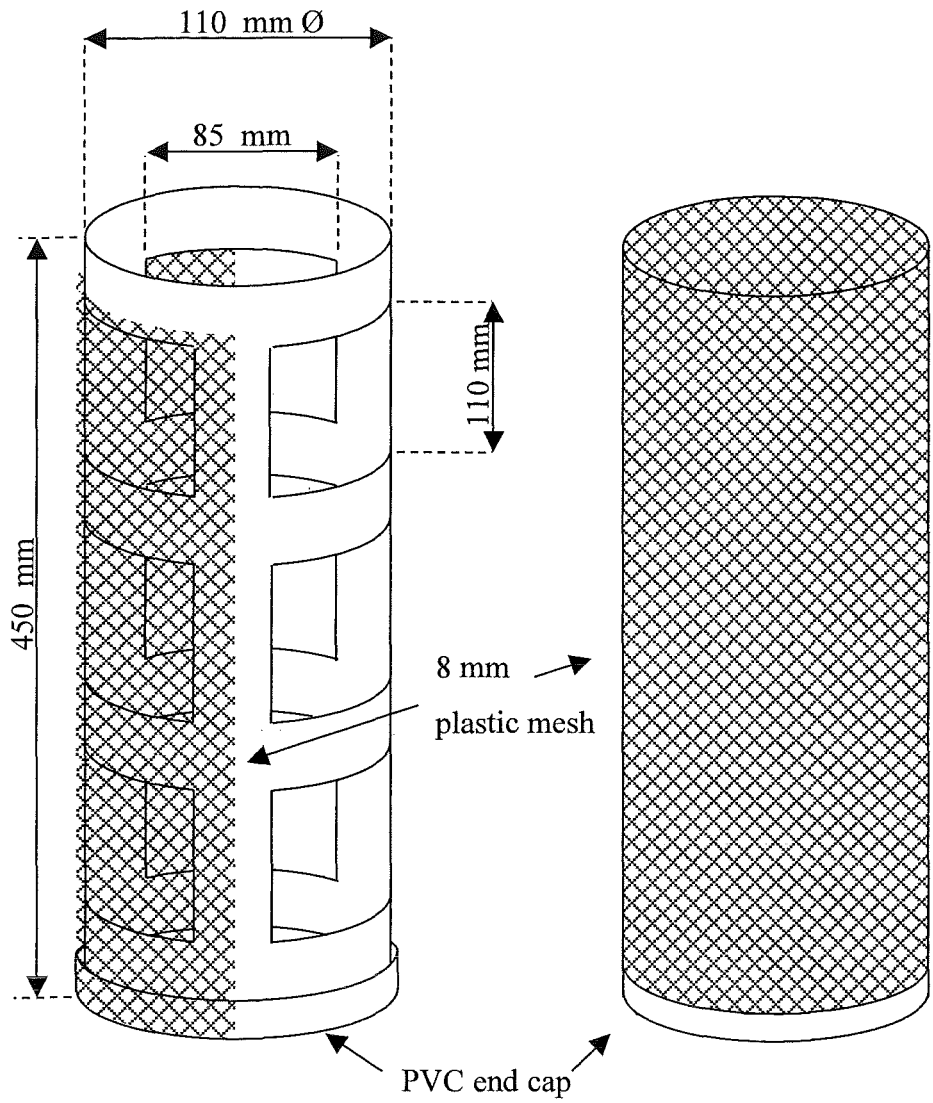

Figure 2. Schematic of colonisation pot design, showing the outer sleeve (*left*, cut-away view) and inner basket (*right*).

basket were again secured with nylon line, filled with fresh gravel and put back in the pot sleeve. Repeated sampling was not undertaken at Sites 3 or 5, because of excessive scouring and bed movement.

Respiration of pot sediment and associated organisms was measured in the laboratory in 1.1 litre respirometers made of 90 mm diameter PVC pipe closed at one end. About one packed litre of sediment was added to each respirometer, which was then filled with Waipara River water at 15°C. Air bubbles were removed by gentle shaking of the respirometer, and the initial dissolved oxygen (DO) concentration of the water was measured to 0.01 mg l^{-1} with a YSI DO meter and probe. Each respirometer was sealed with a press-on cap, to ensure no air gaps remained, and left to incubate on a shaker table in a 15 °C constant-temperature room. DO concentration of the respirometer water was measured after an incubation period of 5-7 hours by removing the respirometer cap and immediately inserting a DO probe into the water. Community respiration was calculated as milligrams of DO consumed per litre of sediment per hour, after adjusting for the DO consumed in a control respirometer containing Waipara River water only.

To compare the contribution of hyporheic (15-45 cm depth) fauna and hyporheic CR to total (0-45 cm depth) fauna and CR, data were expressed in terms of area rather than volume, assuming a surface area at the top of the colonisation pot of 64 cm^2.

Following the measurement of respiration, sediments were washed through a 6 mm mesh sieve onto a 63 μm sieve and preserved in 70% ethanol to which Rose Bengal had been added. Invertebrates were sorted from the sediment, and identified as described above. To determine ash-free dry mass (AFDM) of the remaining organic matter, it was ellutriated from the inorganic sediment, dried at 50 °C for at least 48 hours, weighed, combusted in a muffle furnace at 400 °C for five hours and reweighed. Inorganic sediments < 2 mm diameter were separated from larger particles by wet sieving, dried and weighed. Their weight was then expressed as a percentage of the total sediment weight of the sample.

Data analyses

Data were checked for normality and transformed when necessary. For pump-sampling data, two-way ANOVA was used to compare site and seasonal means of invertebrate abundance, taxonomic richness and physicochemical data. Relationships between

invertebrate abundance, taxon richness and environmental variables were examined using Pearson correlation, rather than multiple regression due to the descriptive, non-manipulative, nature of the study. Correlations were made with summer and winter data separately, since previous work (Chapter 2) had shown that the degree of correlation among variables may depend on seasonal attributes such as flow or temperature. Sequential Bonferroni adjustments of correlation coefficient P-values were made (Rice, 1989), to minimise the likelihood of making type-I errors (rejecting a null hypothesis that is true), whilst maximising statistical power, when multiple hypothesis testing in a large correlation table.

Two-way ANOVA was used also to compare site and depth means for CR, invertebrates, AFDM and % fines collected in colonisation pots. For those sites where sampling was done twice (Sites 1, 4 and 8), three-way ANOVA was used to test for site, depth and sampling occasion effects. Relationships among biological and environmental variables were again examined with Pearson correlation. As the number of correlations made on colonisation pot data were small (less than 20), Bonferroni corrections of P-values were not made.

Invertebrate community composition in well samples and colonisation pots was compared among sites and seasons, using non-metric multidimensional scaling (MDS) on PC-ORD (McCune & Mefford, 1999). Sorensen's index was used as the distance measure in the MDS ordinations. To help interpret the ordinations, axis scores were correlated (Spearman) with invertebrate taxa (P-values were adjusted using sequential Bonferroni correction).

To compare the faunas obtained with the two sampling methods, abundance of each taxon was averaged across all seasons for each site (pump-sampling), or across depths > 15 cm at each site (colonisation pots). The proportion of insect and epigean (insects and snails) taxa to total invertebrate abundance, and the percent dominance of the most abundant taxon were compared between sites and sampling methods using two-way ANOVA. The faunas in samples obtained by the two methods were also classified using Sorensen's index on percentage abundance data linked by group-means (PC-ORD software, McCune & Mefford, 1999).

Results

Physicochemistry

Mean discharge of the Waipara River during the 12 month sampling period was 1.5 $m^3 s^{-1}$, considerably lower than the mean annual discharge, which is 2.5 $m^3 s^{-1}$ (Canterbury Regional Council, 1999). Discharge was lowest during summer (December to late February) when flood frequency (> six-fold increase in flow) was also lowest (Figure 3).

Surface water was absent from Site 1 in March 1999, so a nearby, flowing channel was sampled instead. Mean surface water velocity ranged from 0.07 m s^{-1} (Site 1) to 0.42 m s^{-1} (Site 4) in summer, and was significantly greater in winter ($F = 126.6$, $P < 0.001$), when mean velocities ranged from 0.39 m s^{-1} (Site 1) to 0.95 m s^{-1} (Site 4). Water depth ranged from 0.06 m (Site 1) to 0.20 m (Site 8) in summer and 0.11 (Site 1) to 0.36 m (Site 4) in winter. Water depth was correlated with velocity ($r = 0.74$, $P < 0.001$), and followed the same site and seasonal trends.

Vertical hydraulic gradient (VHG) was generally negative, or downwelling, at all sites except site 4, which had a mean VHG of + 0.02 (Figure 4a). Sites 1 and 7 were regions of strong downwelling (VHG = - 0.41 and - 0.47, respectively), whereas Sites 3 to 6 were either slightly downwelling (VHG = - 0.11 to - 0.08), or upwelling (Site 4). Sites 3 to 5 were in a section of the river constrained by a bedrock canyon, resulting in an elevated water table, and hence more positive VHG. While VHG differed greatly between sites (Table 2), it also varied with season (Table 2). In general, VHG was most positive during autumn and winter, when river discharge was highest. VHG was positively correlated with water depth in winter and velocity in summer (Table 3).

Hyporheic water temperatures ranged from 4.9 – 7.9 °C in winter and 14.7 – 19.4 °C in summer. Site 3 was warmest, and Site 8 was coolest on average (mean = 16.0 °C and 11.8 °C, respectively). Interstitial DO concentrations were generally high (mean = 9.5 g l^{-1}, Figure 4b), and were highest in winter (mean = 11.8 mg l^{-1}) and lowest in summer (mean = 7.6 mg l^{-1}). Site 4, an upwelling site, had the lowest concentration of DO (mean = 7.5 mg l^{-1}, minimum = 3.8 mg l^{-1}), and the greatest difference between surface and hyporheic DO (mean difference = 3.2 mg l^{-1}). The difference between surface and hyporheic DO was positively correlated with VHG and water velocity (Table 3). A negative relationship was found also between DO and VHG, and was stronger in summer than winter (Table 3).

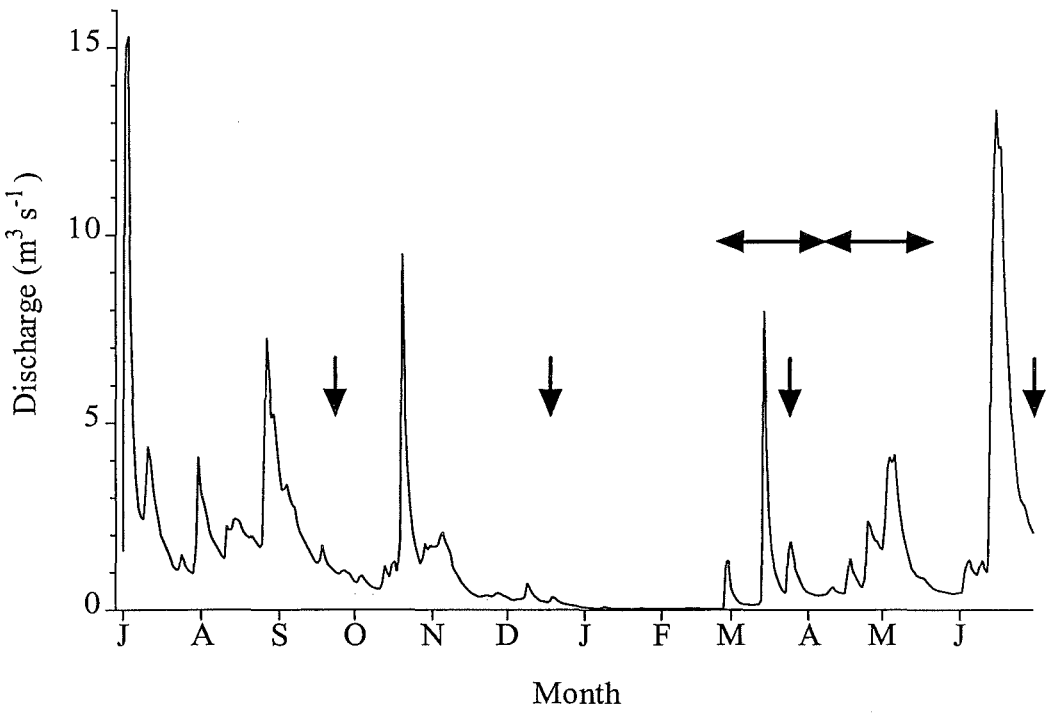

Figure 3. Discharge of the Waipara River between Sites 7 and 8 from July 1998 to July 1999. Vertical arrows mark pump-sampling dates, horizontal arrows mark colonisation pot incubation periods.

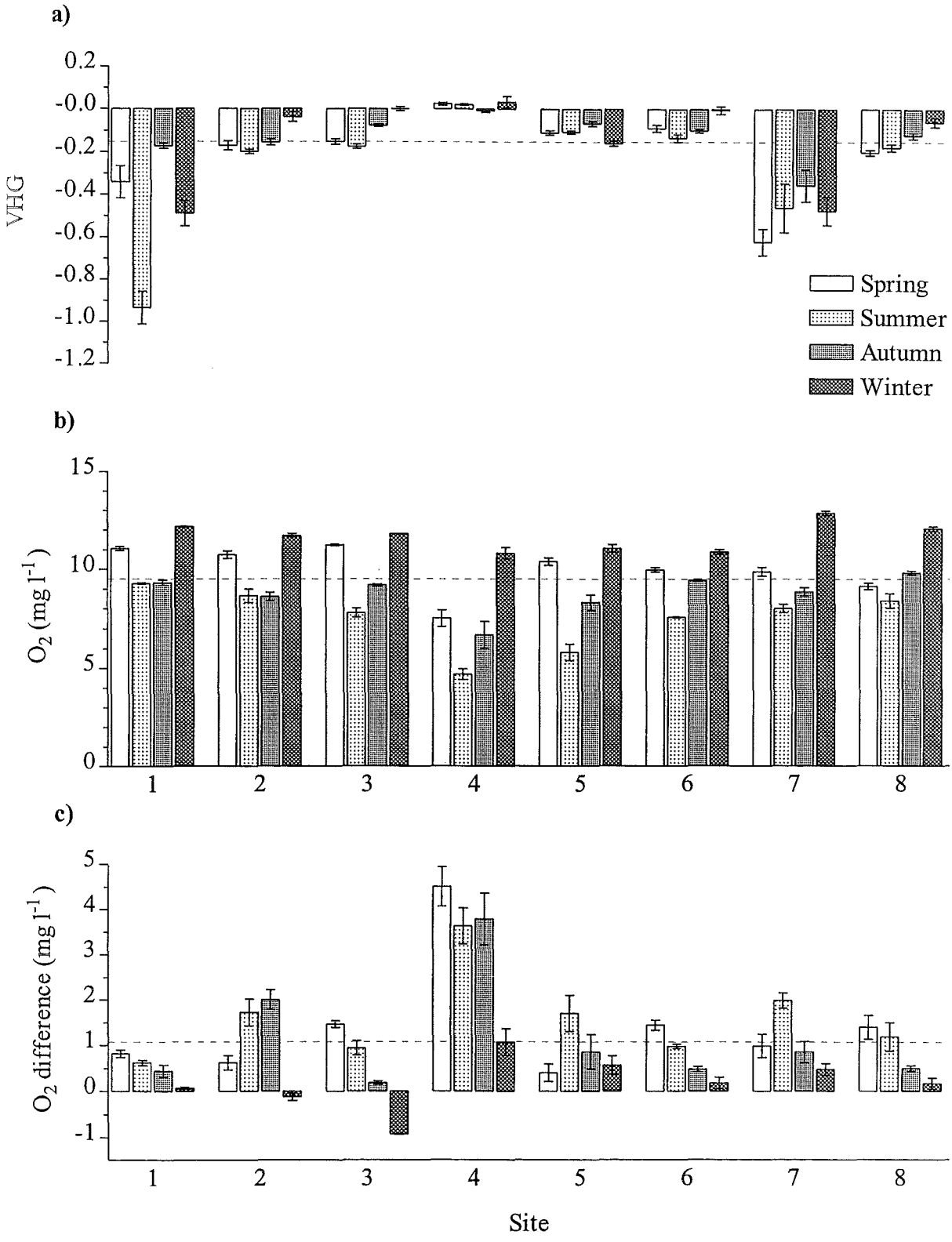

Figure 4. Mean (± 1 SE): a) VHG, b) hyporheic DO, and c) surface minus hyporheic DO taken from 8 hyporheic pump-sampling sites in the Waipara River on four occasions. The dotted horizontal line on each graph indicates the grand mean of all sites and seasons.

Table 2. Results of two-way ANOVA (F-values) between 8 sites and 4 seasons on invertebrate and physicochemical parameters. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, – = not applicable.

Variable	Site	Season	Site * Season
Taxon richness	9.90***	13.61***	0.84
Invertebrate density	18.00***	23.55***	4.85***
DO	63.19***	459.29***	10.20***
DO difference	59.34***	61.69***	6.94***
NTU	14.23***	3.79*	–
VHG	121.50***	23.73***	7.24***
Permeability	5.16***	–	–

Table 3. Pearson correlation coefficients between invertebrate and physicochemical data collected from pump samples. Only significant ($P < 0.05$) correlations, following sequential Bonferroni adjustment, are shown ($n = 77$ comparisons). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Taxon richness and interstitial silt concentration were not significantly correlated with any variables

Variable	Season	Hyporheic DO	VHG	Velocity	Depth
Density	Summer		- 0.54*		
	Winter				
DO	Summer		- 0.74***		
	Winter		- 0.65***		
DO difference	Summer	- 0.79***	0.52*	0.54*	
	Winter				
Temperature	Summer				
	Winter		0.56*		
VHG	Summer			0.55*	
	Winter				0.65***
Permeability	Summer				0.57**

Surface and hyporheic DO were most similar during winter (Figure 4c), when discharge was greatest (Figure 3).

Sites 4 -7 had the highest interstitial turbidity (means = 4 500 – 5 200 NTU), while Site 3 was least turbid (mean = 1 100 NTU). Interstitial turbidity showed a weak seasonal trend to be higher in summer than winter (Figure 5a, Table 2). Turbidity was positively correlated with the concentration of interstitial fines < 63μm diameter ($r = 0.76$, $P < 0.001$). When fines were separated into silt-sized particles (2 - 63 μm) and clay-sized particles (< 2 μm), a stronger correlation was found between clay and turbidity ($r = 0.77$, $P < 0.001$) than between silt and turbidity ($r = 0.59$, $P < 0.001$).

Streambed permeability was measured only during spring and summer, since the Terhune standpipe was broken at other times. Mean permeability was 32 cm minute^{-1}, and ranged from a minimum of < 1 cm minute^{-1} at Site 1, to 11.1 m minute^{-1} at Site 3 (Figure 5b). Permeability was positively correlated with water depth (Table 3).

Invertebrate community

(a) Pump samples

In total 46 023 invertebrates were collected from 159 pump-samples. The river community was strongly dominated by non-insect taxa, with crustaceans being particularly common (Table 4). Harpacticoid copepods were especially abundant, and comprised 45 % of all animals caught. The subterranean amphipod *Paraleptamphopus subterraneus* and larval mites (Acari) were also abundant. While few other taxa were found in high densities, many occurred in a large number of samples; four taxa occurred in more than 90 % of all samples, and nine occurred in at least 50 % of samples (Table 4).

On average, 164 individuals and 12 taxa were taken per 5-litre pump sample (mean of all sites and seasons), and significant differences in both abundance and taxon richness were found between sites and seasons (Table 2). Site 4 had the lowest mean abundance (63 individuals per 5 litres) and Site 3 the highest (461 per 5 litres, Figure 6a). The greatest number of invertebrates collected from a single 5 litre sample was at Site 1 in summer, when 1808 harpacticoids and 1300 larval mites contributed to a total invertebrate catch of 3560 individuals. In contrast, Site 1 had the lowest mean taxon richness (9 taxa

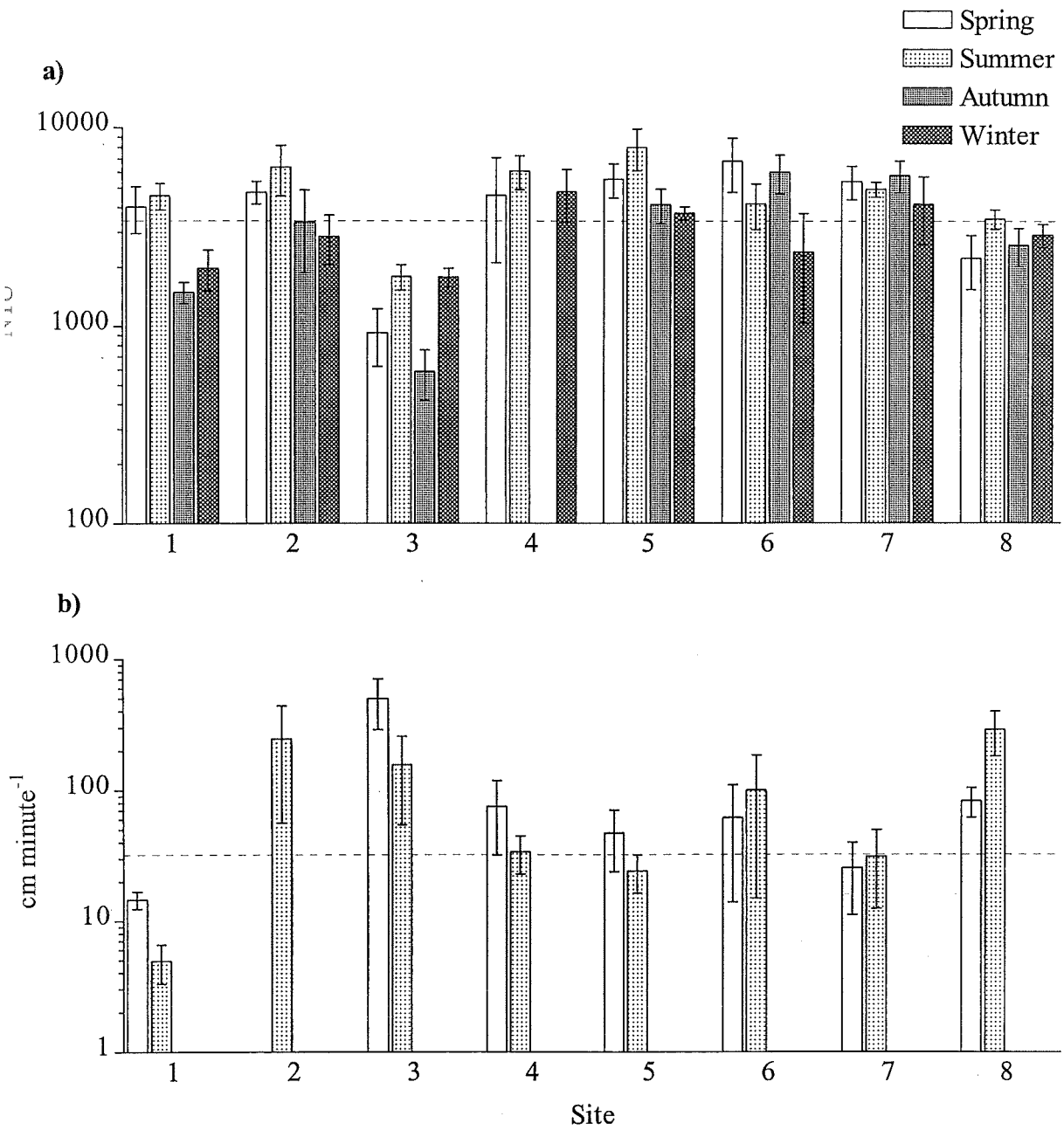

Figure 5. Mean (± 1 SE): a) interstitial turbidity and b) hyporheic permeability from 8 hyporheic pump-sampling sites in the Waipara River. The dotted horizontal line on each graph indicates the grand mean of all sites and seasons.

Table 4. Frequency of occurrence, percentage abundance, and mean abundance per 5 litre sample of the most common hyporheic invertebrates collected in 159 pump-samples from the Waipara River.

Taxon		Frequency (%)	Abundance (%)	Abundance (mean no. 5 l^{-1})
Harpacticoida	(Copepoda)	98.7	45.4	132.1
Paraleptamphopus subterraneus	(Amphipoda: Eusiridae)	96.9	13.0	37.9
Cyclopoida	(Copepoda)	91.8	7.6	22.3
Oligochaeta		91.8	7.1	20.7
Acari larvae		80.5	14.8	43.0
Nematoda		77.4	1.1	3.2
Ostracoda		75.5	2.2	6.4
Syncaridae		69.2	1.4	3.9
Acari sp. 'g'		53.5	1.2	3.5
Acari indet		49.1	0.6	1.6
Heterias sp.	(Isopoda: Janiridae)	48.4	2.2	6.3
Cruregens fontanus	(Isopoda:Anthuridae)	43.4	0.4	1.1
Acari sp. 'n'		39.6	0.4	1.2
Phreatogammarus fragilis	(Amphipoda: Gammaridae)	31.4	0.2	0.6
Tricladida	(Turbellaria)	28.3	0.2	0.5
Cladocera		25.8	0.7	2.2
Orthocladiinae	(Diptera: Chironomidae)	24.5	0.2	0.7
Hydora sp. (larvae)	(Coleoptera: Elmidae)	22.6	0.2	0.6
Potamopyrgus antipodarum	(Gastropoda: Hydrobiidae)	19.5	0.2	0.6
Polycentropodidae	(Trichoptera)	18.2	0.1	0.4

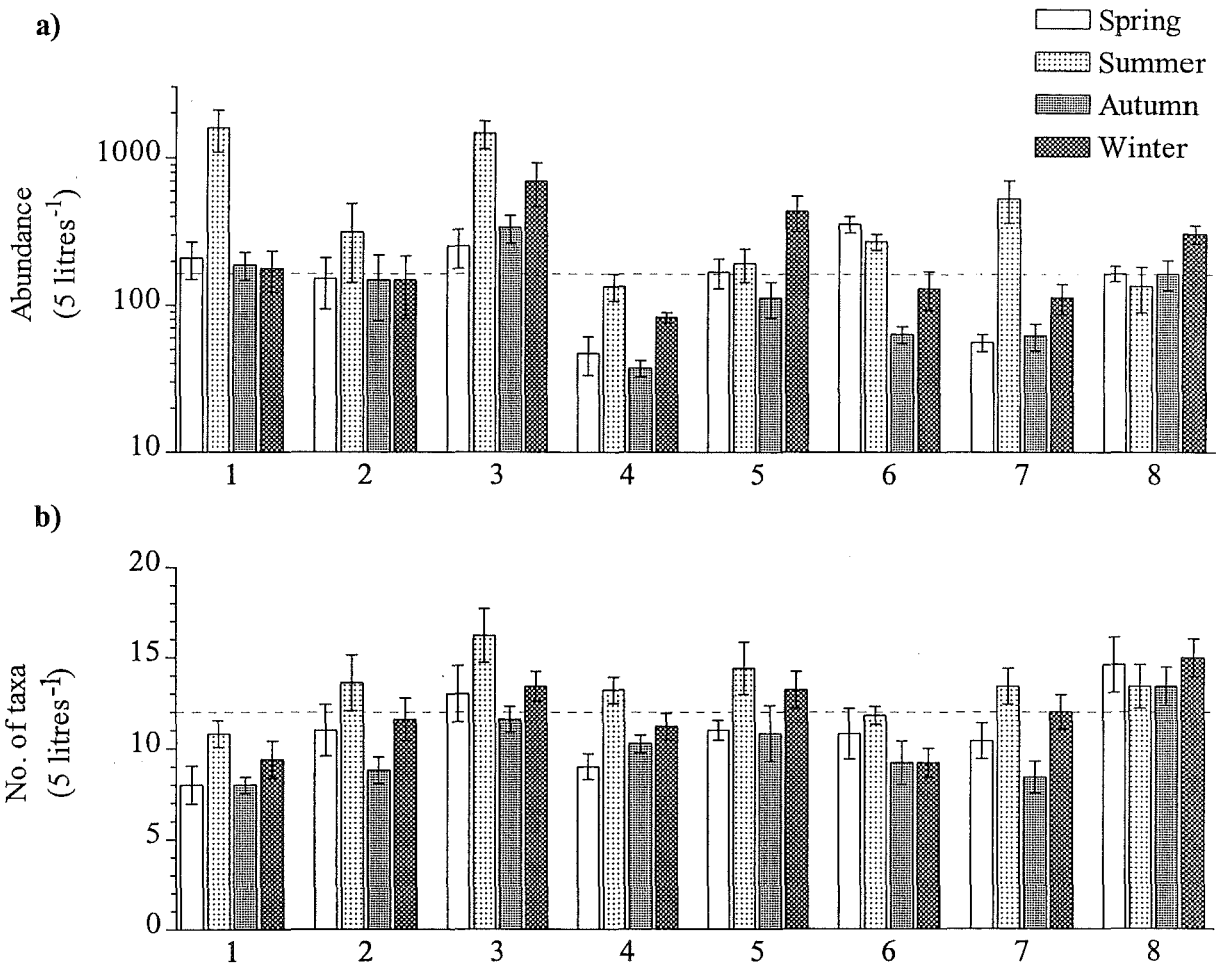

Figure 6. Mean (± 1 SE): a) abundance and b) taxon richness of invertebrates in pump samples taken at eight sites in the Waipara River on four occasions. The dotted line on each graph indicates the grand mean of all sites and seasons.

per 5 litres), while Site 8 had the highest (14 per 5 litres, Figure 6b). Both taxon richness and invertebrate abundance were greatest during summer.

Invertebrate abundance was negatively correlated with VHG in summer, but not winter (Table 3). Neither invertebrate abundance nor taxon richness were significantly correlated with any other measured variables.

Ordination of the invertebrate community yielded a two-dimensional solution with low stress (0.14), indicating a reasonable relationship between the original dissimilarity matrix and distance in the reduced 2-dimensional ordination space (Clarke, 1993). Seasonal samples from Sites 1 and 2 formed distinct groups, but the other site-season data points overlapped considerably (Figure 7). Axis 1 scores were negatively correlated with the abundance of harpacticoids (r_s = - 0.82, P < 0.001), larval Acari (r_s = - 0.67, P = 0.001), and oligochaetes (r_s = - 0.61, P = 0.008). Axis 2 scores were also negatively correlated with harpacticoids (r_s = - 0.61, P = 0.008), as well as *Hydra* sp. (r_s = - 0.67, P = 0.001) and *P. subterraneus* (r_s = - 0.71, P < 0.001). The magnitude and direction of community assemblage change was greatest at most sites between spring and summer, indicated by a shift towards the bottom of Figure 6 between these seasons. This change was due to the increased abundance of harpacticoids, *Hydra* sp. and *P. subterraneus* in summer.

(b) Colonisation pots

Invertebrate abundance differed significantly between sites (F = 27.9, P <0.0001), depths (F = 8.9, P = 0.0003), and sampling occasions (F = 94.7, P < 0.0001). Mean abundance was greatest at Site 3 (432 individuals per litre of sediment), and lowest at Site 1 on the first sampling occasion (13 individuals per litre) when flow was intermittent (Figure 8a). Mean abundance, including all sites, declined from 227 individuals per litre at 0-15 cm, to 123 and 87 individuals per litre at 15-30 cm and 30-45 cm depths, respectively. Invertebrate abundance was higher on the second sampling occasion at Sites 1 and 4, but did not change at Site 8 (Figure 8a).

Taxonomic richness also differed significantly between sites (F = 8.9, P < 0.0001), depths (F = 8.4, P = 0.0004) and sampling occasions (F = 51.4, P < 0.0001). Mean taxon richness was greatest at Site 8 on the second sampling occasion (14 taxa per litre) and poorest at Site 1 on the first sampling occasion (6 taxa per litre, Figure 8b). On average, taxon richness declined from 13 taxa per litre at 0-15 cm to 10 and 9 taxa per litre at 15-30 cm and 30-45 cm depths, respectively. Taxon richness was higher on the second sampling

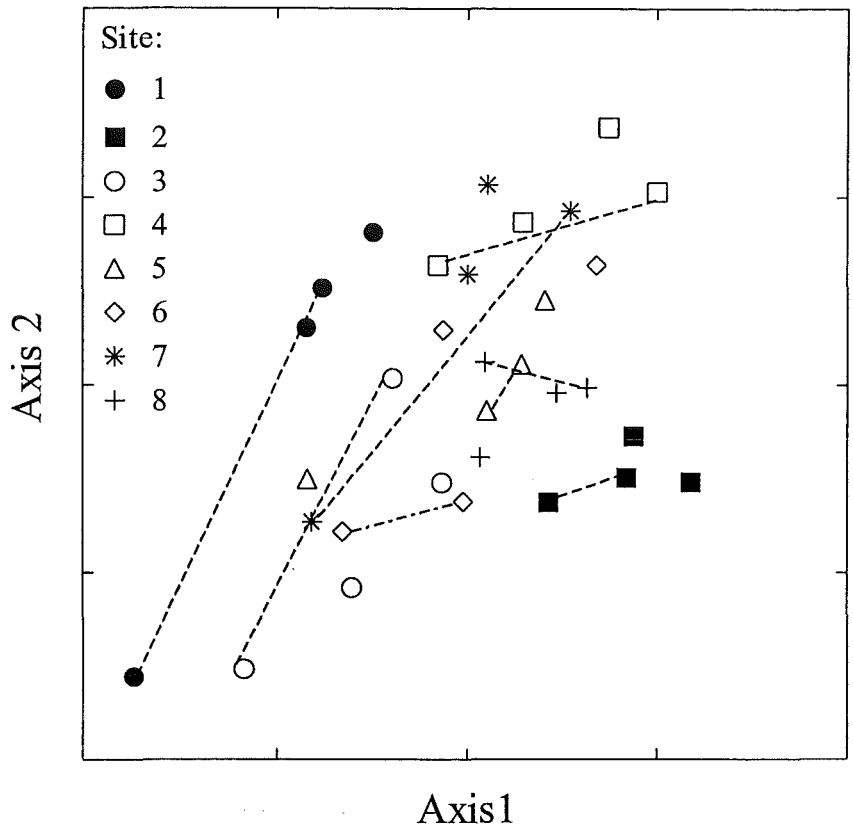

Figure 7. MDS ordination of hyporheos collected by pump-sampling in the Waipara River in four seasons (stress = 0.14). Vectors join spring and summer sample means at each site.

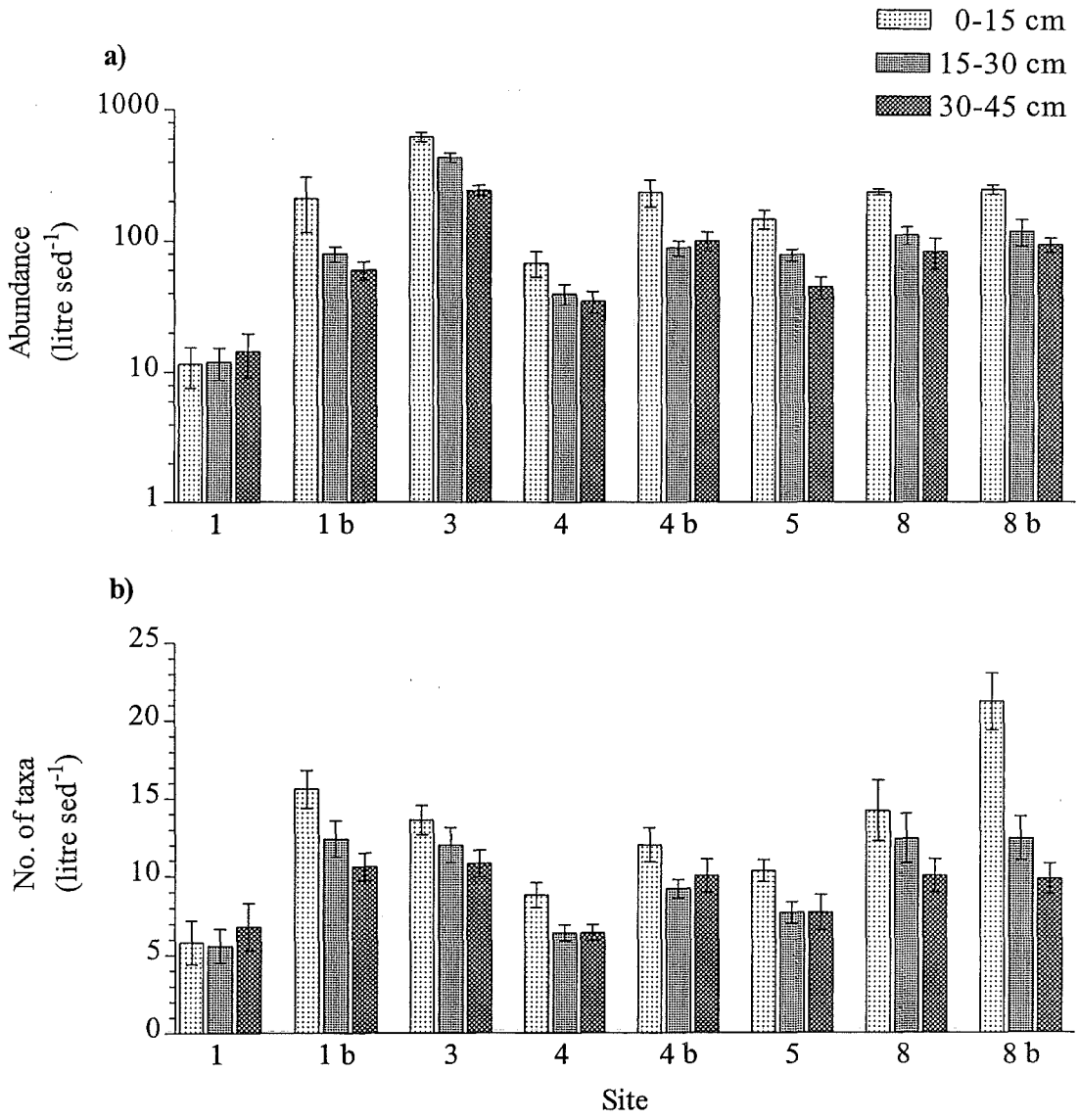

Figure 8. Mean (± 1 SE): a) abundance and b) taxon richness of invertebrates in colonisation pots from five sites after a six week colonisation period in the Waipara River. All data collected in April, except those labeled 'b', which were collected in May. There was a six week colonisation period.

occasion at all three resampled sites (Figure 8b), although the strongest increase occurred at Site 1, where numbers of taxa doubled from 6 to 12 per litre.

Ordination of colonisation pot invertebrate community data yielded a two-dimensional solution with very low stress (0.08). The community at all depths at Site 1 formed a separate cluster on both sampling occasions, while Site 4 was distinct from other sites only during the first sampling (Figure 9). Axis 1 scores were most strongly and positively correlated with abundance of the snail, *Potamopyrgus antipodarum* ($r_s = 0.90$, $P < 0.001$) and ostracods ($r_s = 0.80$, $P < 0.001$). Axis 1 scores were also significantly and positively correlated ($r_s > 0.62$, $P < 0.05$) with *Hydora* sp. (Coleoptera: Elmidae), oligochaetes, tardigrades, mites and the snail *Physa acuta*. These taxa became less abundant with depth, as indicated by a right to left shift in ordination space. Axis 2 scores were positively correlated with *P. subterraneus* ($r_s = 0.66$, $P = 0.02$) and negatively correlated with tardigrades ($r_s = - 0.73$, $P = 0.002$) and Collembola ($r_s = - 0.64$, $P = 0.03$).

The much greater abundance of *P. subterraneus* at Site 4 during the first sampling occasion, explains its separation from the other sites on the ordination plot (Figure 9). The placement of Site 1, occasion 2, low on axis 2 was due to its relatively high abundance of tardigrades and Collembola (Figure 9). The separation of Site 1, sampling 1, to the left of the ordination was associated with its overall low faunal abundance and taxon richness.

Community Respiration

Community respiration (CR) declined significantly ($F = 50.0$, $P < 0.0001$) with depth at all sites (Figure 10a), with the strongest decline occurring between the 0 - 15 cm and 15 - 30 cm depth strata (means = 0.65 and 0.40 mg O_2 litre sediment^{-1} hr^{-1}, respectively). CR continued to decline between the medium and deep substrates at Sites 1 and 3, but not at Sites 4, 5 and 8, where it did not differ between medium and deep substrata (ANOVA depth x site interaction, $F = 2.9$, $P = 0.009$). Overall, respiration was greatest at Site 3 and lowest at Sites 4 and 5. Although surface flow was only intermittent at Site 1, CR at Site 1 was within the range of values recorded for sites with perennial flow (Figure 10a). CR was significantly higher on the second sampling occasion at Sites 1 and 4, but lower at Site 8 (ANOVA occasion x site interaction, $F = 10.2$, $P = 0.0001$, Figure 10a).

AFDM also declined with depth (Figure 10b) and was positively correlated with CR ($r = 0.72$, $P < 0.001$, Figure 11a), as was invertebrate abundance, except on the first sampling occasion at Site 1. The absence of surface water at that time resulted in very few

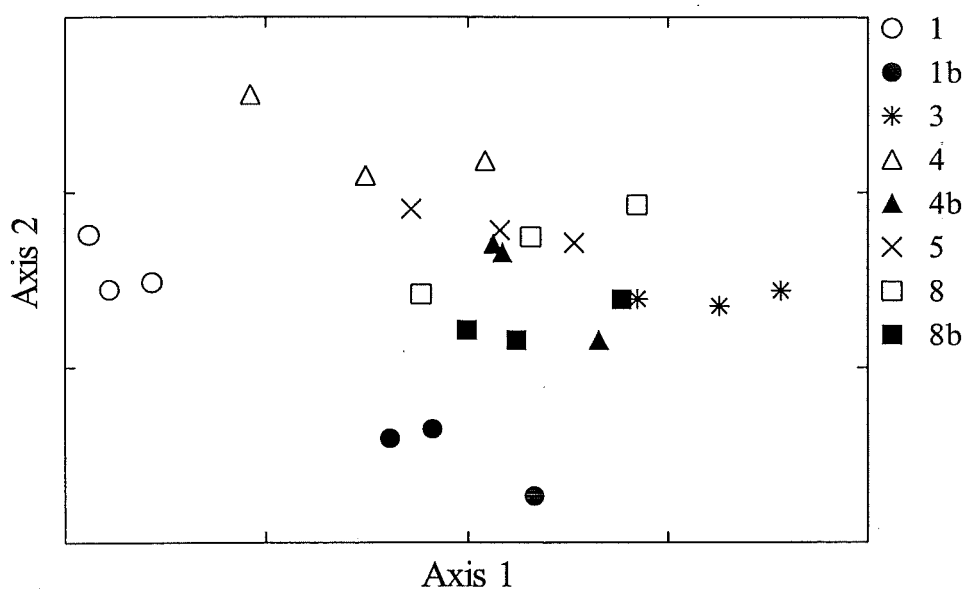

Figure 9. MDS ordination of hyporheos collected from colonisation pots at five sites in the Waipara River (stress = 0.08). All data collected in April 1998, except those labeled 'b' (closed symbols), which were collected in May 1998

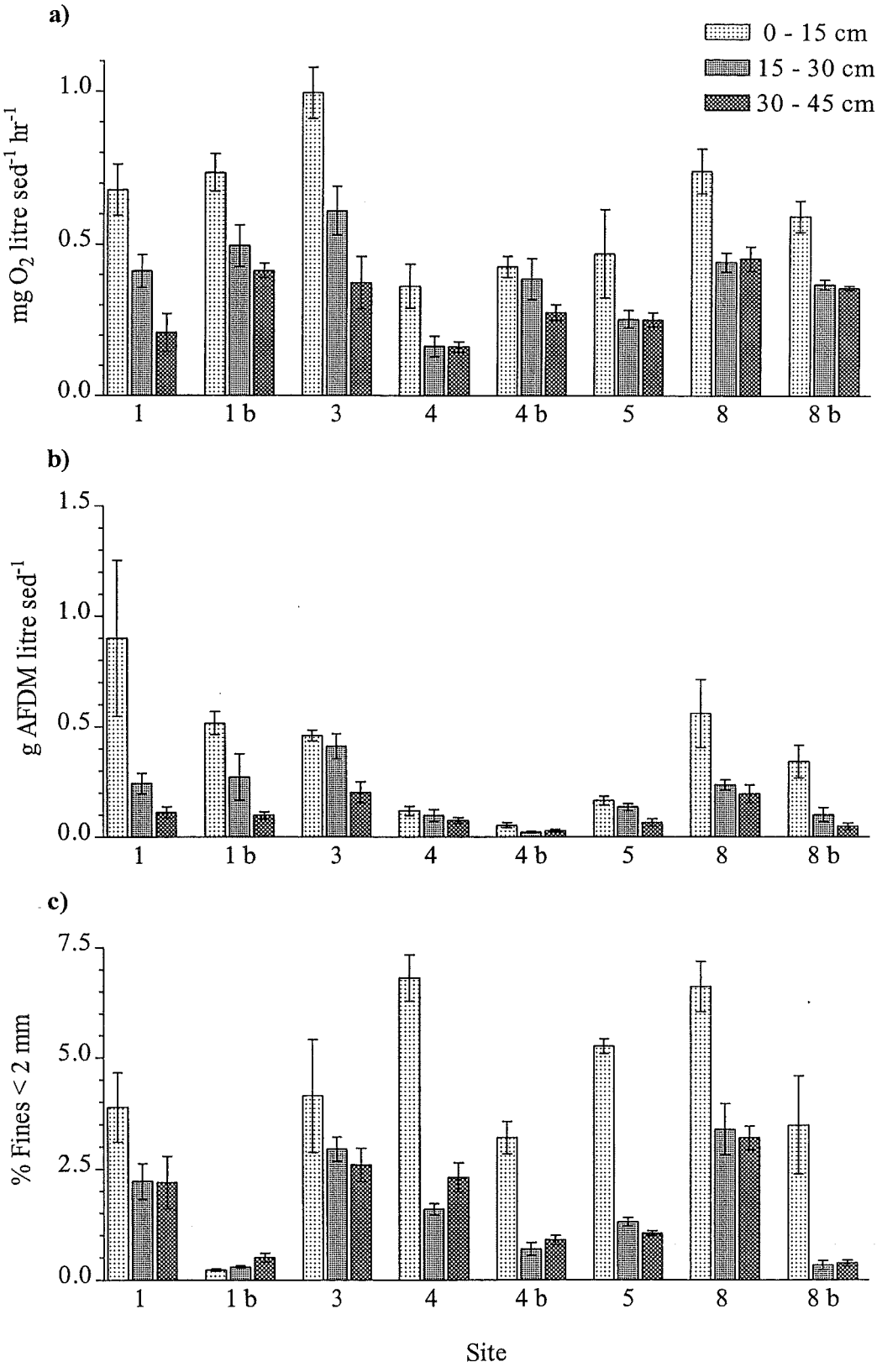

Figure 10. Mean (± 1 SE): a) community respiration, b) AFDM, and c) % fines in colonisation pots from five sites in the Waipara River. All data collected in April, except those labeled 'b', which were collected in May.

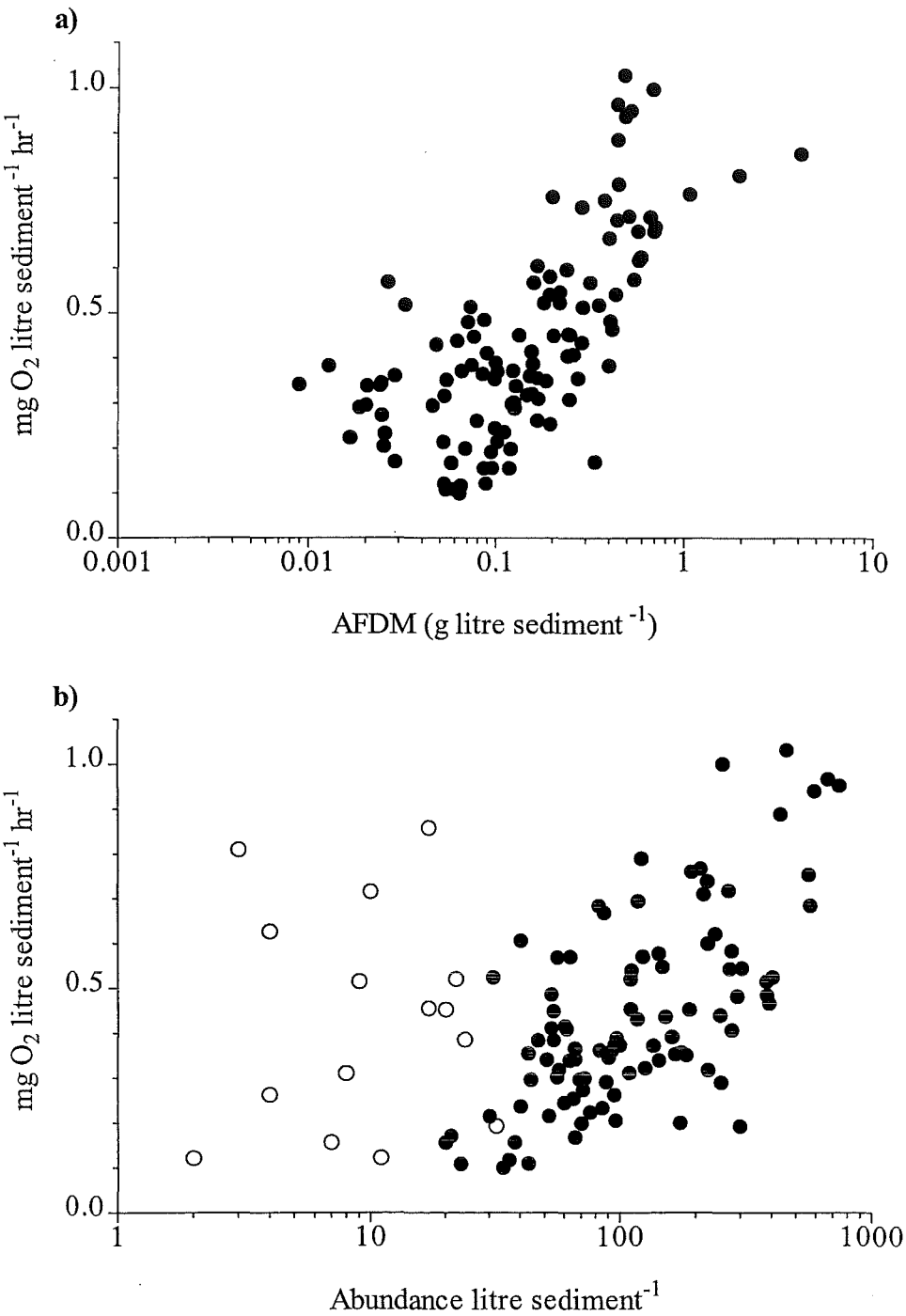

Figure 11. Relationships between community respiration and a) AFDM and b) invertebrate abundance in colonisation pots at 5 sites in the Waipara River sampled in April and May. Open symbols in plot (b) are values for Site 1 from May.

invertebrates being present. Because of this, the inclusion of Site 1, occasion 1 data resulted in the correlation between invertebrate abundance and CR being lower ($r = 0.50$, $P < 0.001$), than when these data were omitted ($r = 0.70$, $P < 0.001$, Figure 11b).

The percentage (by dry weight) of fine sediments < 2mm diameter was greatest between 0-15 cm (mean = 4 %, Figure 10c). Percent fines was not correlated with pot respiration or invertebrate abundance, but showed a weak positive correlation with AFDM ($r = 0.26$, $P < 0.01$). In contrast, CR at depths of 0-15 cm and 15-30 cm was strongly and negatively correlated ($r = -0.99$ and -0.98, $P < 0.01$) with interstitial turbidity measured by pump-sampling from 30 cm at each site (Figure 12a). However, CR at 30-45 cm was not significantly correlated with turbidity ($r = -0.64$, $P > 0.05$). Invertebrate abundance was negatively correlated with turbidity at all depths among sites with surface flow ($r \geq 0.96$, $P < 0.05$), but not at Site 1, where flow was absent (Figure 12b).

The contributions of hyporheic (15 - 45 cm) to total (0 - 45 cm) CR and invertebrate density estimated from pot samplers at each site were remarkably similar (Table 5). The hyporheic component contributed about 50% to total invertebrate abundance and CR per unit area at each site.

Comparison of Sampling Methods

The colonisation pot and pump-sampling methods enabled similar conclusions to be reached in terms of ranking sites according to invertebrate abundance and taxon richness. Both methods ranked the sites from highest to lowest invertebrate abundance and taxon richness in the order: 3, 8, 5, 4, 1. However, the composition of the fauna sampled by each method was extremely different, with very little overlap in species occurrence, and no similarity in terms of the dominant taxa sampled (Figure 13). While larval mites, *Paraleptamphopus subterraneus* and harpacticoids made up over half the fauna sampled by pumping, the snail *Potamopyrgus antipodarum* and tardigrades dominated the hyporheic fauna of the colonisation pots (Figure 13). Colonisation pots had significantly more epigean taxa than pump samples (44% vs 1%; $F = 134.5$, $P < 0.001$), and a higher proportion of insect taxa (6% vs 1%; $F = 24.6$, $P < 0.001$). The most dominant taxon in colonisation pots was generally more dominant than in pump samples (49% vs 41%), except at Site 1 where harpacticoids dominated the pump-sampling fauna to a greater degree (58 %) than at other sites.

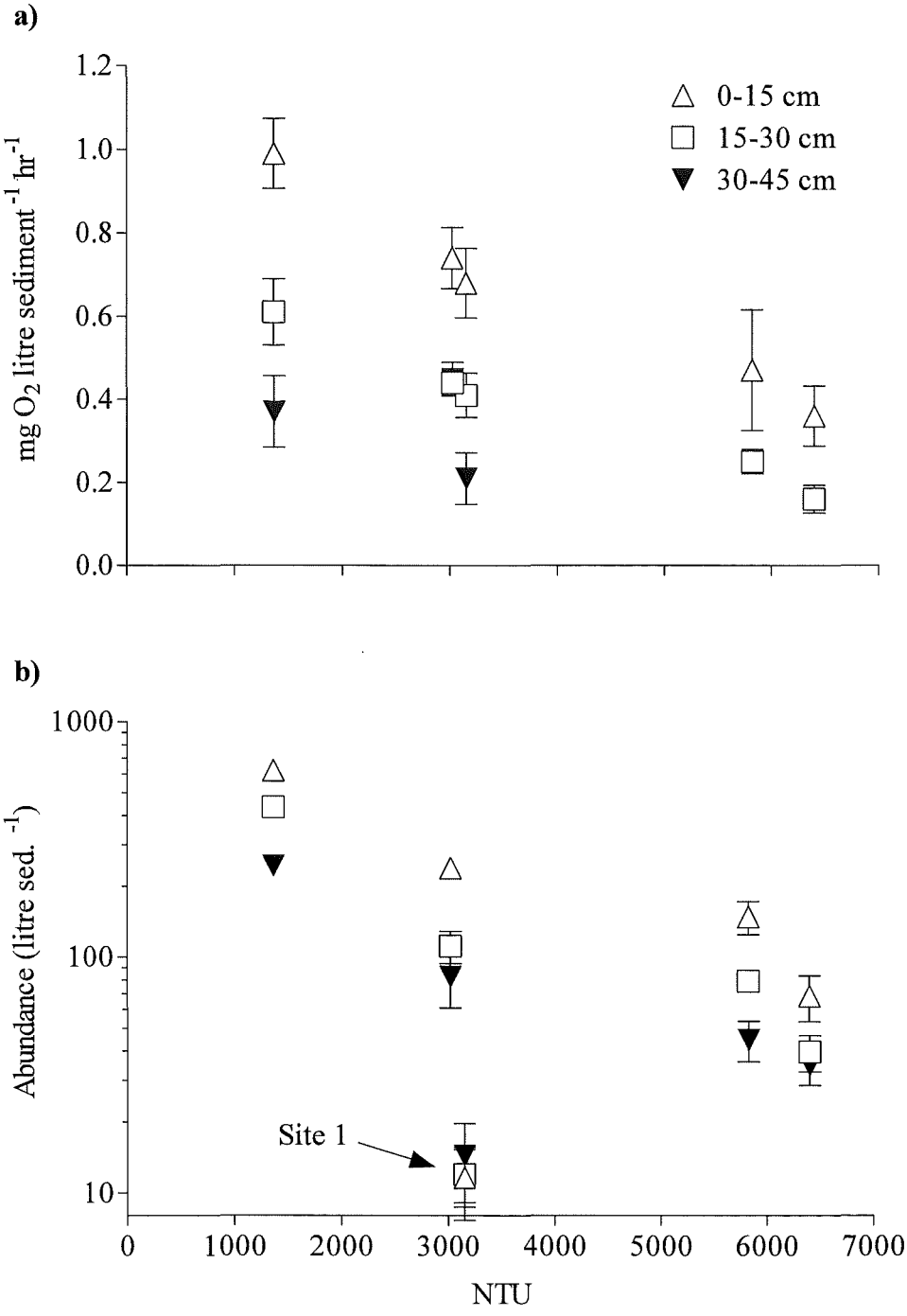

Figure 12. Mean (± 1 SE) a) community respiration and b) abundance of invertebrates in colonisation pots (per litre of sediment) in May plotted against mean interstitial turbidity (NTU; measured by pump-sampling wells), at 5 sites in the Waipara River.

Table 5. The contribution of hyporheic (15-45 cm) to total (0-45 cm) community respiration and invertebrate density, calculated for five sites in the Waipara River using colonisation pot data.

Site	Community Respiration			Invertebrate Density		
	Hyporheic	Total	Hyporheic/	Hyporheic	Total	Hyporheic/
	($g\ O_2\ m^{-2}\ hr^{-1}$)		Total (%)	(No. m^{-2})		Total (%)
1	0.12	0.23	52	13 080	30 570	43
3	0.15	0.31	50	106 480	203 870	52
4	0.08	0.14	56	20 780	44 810	46
5	0.08	0.15	52	19 440	42 650	46
8	0.13	0.23	55	31 930	70 220	45
Mean	0.11	0.21	53	38 340	78 430	46

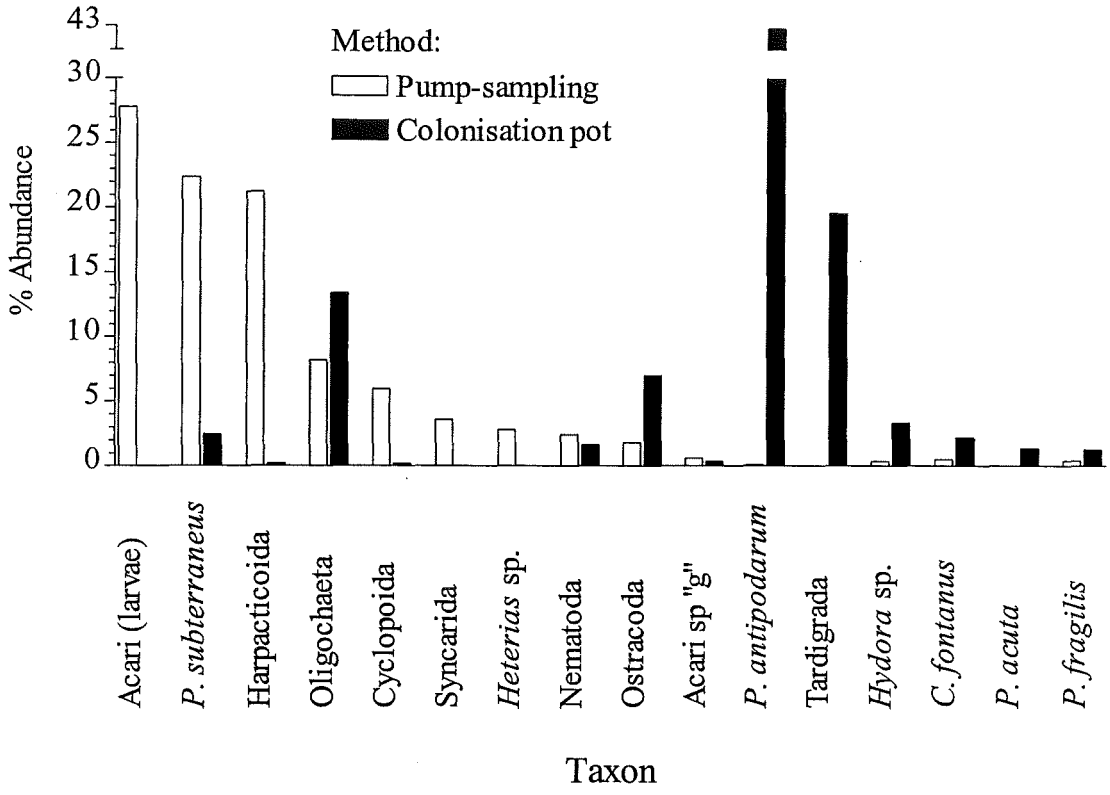

Figure 13. Relative abundance of the most common taxa collected by pump-sampling (depth = 30 cm) and colonisation pot methods. Data are from sites 1, 3, 4, 5, and 8. Colonisation pot data is taken from 15-45 cm depth.

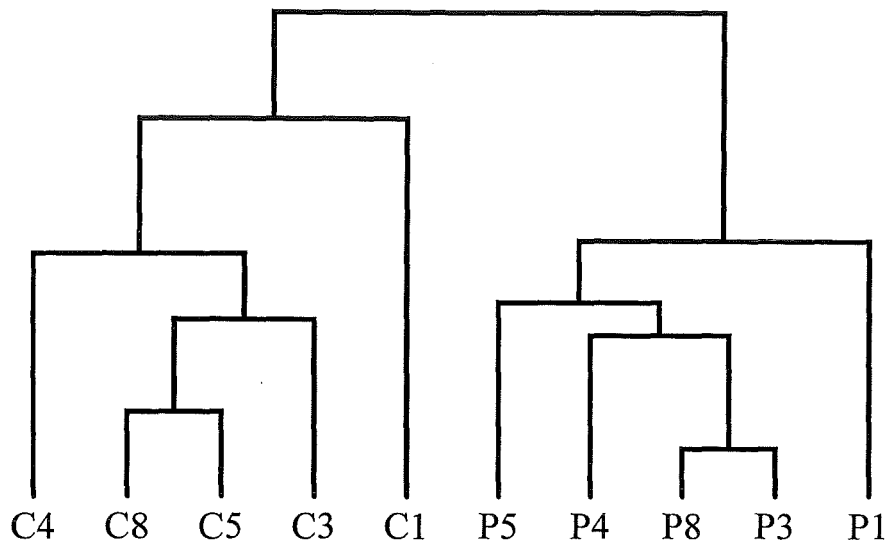

Figure 14. Cluster analysis of hyporheic communities from 5 sites in the Waipara River, using Sorensen's index on percentage abundance data and linked by group averages. Samples were collected by pump-sampling ('P' prefix) and in colonisation pots ('C' prefix). Colonisation pot data exclude the 0-15 cm depth.

Cluster analysis of invertebrate communities at the five sites showed two principal groups representing the pump and pot sample assemblages (Figure 14). The first division of these two large groups separated Site 1 from the remaining sites, but other groupings were not consistent between sampling methods.

Discussion

Hydrology-invertebrate interactions

The majority of sites sampled in the Waipara River were downwelling. Because of this, and the high permeability of the sediments, the difference between surface and hyporheic dissolved oxygen (DO) concentration was generally very low. However, the difference was greater during low flow periods, presumably due to longer hyporheic residence times of channel water. Depth and velocity showed positive relationships with permeability and VHG, and VHG was negatively correlated with invertebrate density. As invertebrate abundance showed a negative correlation with VHG during summer but not winter, it seems likely that longer hyporheic residence times during low flow also negatively affect the biota. During times of high river flow, groundwater levels are also higher, and there is a greater flow of surface water through the hyporheic zone (Freeze & Cherry, 1979; Fraser & Williams, 1998). This explains why shorter hyporheic residence times in the Waipara resulted in highly oxygenated interstices, despite VHG being greater during higher-flow months. Numerous authors have reported a negative effect of increased hyporheic residence time on invertebrate abundance (see reviews by Findlay, 1995; Brunke & Gonser, 1997; Ward et al., 1998), although the interplay between residence time and VHG has not been examined previously.

In addition to channel flow, interstitial permeability is related to sediment particle size and packing (Freeze & Cherry, 1979). In the Waipara, interstitial turbidity (a measure of silt concentration) was negatively correlated with invertebrate abundance and community respiration of sediments from colonisation pots. In contrast, turbidity was not correlated with the abundance or taxonomic richness of invertebrates collected by pump-sampling. However, taxon richness was greatest at Site 3 where turbidity was lowest and permeability highest, while richness was lowest at Site 1 where permeability was lowest. These data suggest that greater interstitial spaces allowed the infiltration of more taxa

where permeability was high. Maridet et al. (1996) and Richards & Bacon (1994) also found that bed porosity and fine sediment concentration were primary factors limiting the abundance of hyporheic invertebrates in the rivers they studied, although in a survey of 14 sites in the United States Strayer et al. (1997) found the relationship between particle size and invertebrate abundance to be relatively weak. In a comprehensive review, Brunke & Gonser (1997) suggested that colmation, the clogging of sediment interstices by fine sediment, reduces surface-hyporheic connectivity, and may therefore reduce the penetration of solutes and invertebrates into the substrate. The effect of fine sediment on hyporheic communities is further examined in a field experiment described in Chapter 6.

Community respiration

Community respiration (CR) was correlated with AFDM and invertebrate abundance, and all three generally declined with depth. Pusch & Schwoerbel (1994) and Brunke & Fischer (1999) reported similar correlations between these variables and Brunke (1999) suggested that a filtering-out of organic matter, microbes and invertebrates might occur with increasing depth into the substrate. Sites 4, 5 and 8 did not follow the pattern of continuous decline in CR with depth, suggesting local differences in flow path, perhaps due to differences in substrate heterogeneity or packing, may cause small-scale (i.e., colonisation pot scale) variations in the relationship between POM, biological activity and depth.

The hyporheic zone (to 42 cm depth) contributed to 40-50% of total stream respiration in a desert stream in Arizona (Grimm & Fisher, 1984) and 70% of the whole stream metabolism of Buzzard Branch (to 20 cm depth), a sandy-bottomed black-water stream (Fuss & Smock, 1996). In streams with coarser, more permeable sediments, the rate of oxygen renewal and organic matter supply to the hyporheic zone is expected to be higher, and the contribution of hyporheic to whole-stream metabolism is therefore expected to be greater (Findlay, 1995). Thus, the hyporheic zone contributed 76-96% of whole stream metabolism in the River Necker, a gravel-bed river in Switzerland (Naegeli & Uehlinger, 1997), and 40-93% of whole stream respiration in two stony streams in New Mexico (Fellows et al., 2001). Both these studies estimated hyporheic respiration as the difference between whole stream respiration (using diel oxygen curves) and respiration in benthic chambers. The hyporheic contribution to total CR was 52-56% in the Waipara River, which is towards the low end of what might be expected in a gravel bed river with

high permeability. However, the benthic (upper 15 cm) component of total CR in the Waipara was 2-10 times the depth measured in comparable studies (see references above), and could explain in part the lower contribution of hyporheic to total CR. In addition, the vertical and horizontal limits of the hyporheic zone were not known in the Waipara, and may have extended well beyond the 45 cm depth measured in this study.

The vertical and horizontal extent of the hyporheic zone has been identified in numerous rivers by chemical (e.g., alkalinity, conductivity and oxygen) or temperature discontinuities between channel water and groundwater (Triska et al., 1989; Williams, 1989; Stanford & Ward, 1988; White, 1993; Fraser & Williams, 1998). Triska et al. (1989) defined the lower limit of the hyporheic zone as the area below the streambed containing <10% advected channel water. In the Waipara, dissolved oxygen concentration at 30 cm depth averaged 89% of surface water, suggesting that the hyporheic zone most likely extended well below the 45 cm depth sampled by colonisation pots.

Flow intermittency

When surface flow was absent from Site 1, hyporheic invertebrate abundance and taxonomic richness were considerably lower than at flowing sites. The presence of surface water during the second sampling of Site 1 coincided with increased invertebrate abundance and richness, although the fauna was dominated by different taxa than other sites, and collembolans were particularly abundant. In several Sonoran Desert streams, Boulton et al. (1992) also found a distinct invertebrate fauna associated with what they called the dry channel hyporheic biotope. The persistence of invertebrates in desert streams with a high frequency and intensity of flooding and drying has been attributed to their ability to recolonise disturbed sites rapidly (Stanley et al., 1994). Clinton et al. (1996) found that invertebrate abundance increased in hyporheic wells as surface water was lost, and suggested that the hyporheos used the hyporheic zone as a refuge to avoid desiccation at the surface. However, del Rosario & Resh (2000) found no increase in the abundance of surface taxa in the hyporheic zone of an intermittent Californian stream as it dried up, and concluded that the hyporheic zone did not serve as a refuge from drying for surface taxa. McLeod (1998) also concluded that the hyporheic zone did not serve as an invertebrate refuge from drying in an intermittent reach of Middle Bush Stream, New Zealand. As the hyporheic fauna at Site 1 in the Waipara contained proportionally fewer surface taxa

present at flowing sites, the hyporheic zone did not appear to be a refuge for surface invertebrates from drying.

Community respiration at the intermittently-flowing Site 1 was similar to that at the flowing sites, despite sediments being less saturated and interstitial flow being reduced. The lack of surface water during the first sampling occasion resulted in far fewer invertebrates being collected than at the second sampling when surface water was present. Because very few invertebrates were present during the first sampling, CR at site 1 must have been almost entirely attributable to microbial respiration. To the best of my knowledge, no other study has measured hyporheic microbial activity in response to drying or re-wetting. However, studies elsewhere in New Zealand (Graesser, 1988), England (Douglas, 1958) and North America (e.g. Peterson, 1987; Blinn et al., 1995) found benthic algal production declined when subjected to periods of aerial exposure.

In Queensland, Australia, Mossisch (2001) found desiccation reduced epilithic chlorophyll *a* concentration in one stream, but not another, and that epilithic ash-free dry mass was unaffected by desiccation in both streams. Mossisch suggested that desiccated diatoms in one stream, and a greater mass of detritus in the other, resulted in the null effect of drying on epilithic biomass. Mats of filamentous algae may also act as 'sponges', and prevent desiccation of epilithic communities beneath them during periods of aerial exposure (Usher & Blinn, 1990). At Site 1 in the Waipara River, detritus and decaying mats of filamentous algae accumulated when there was no surface flow and resulted in high values of AFDM above 15 cm depth. The accumulation of organic matter in surface sediments at Site 1 may therefore have served to trap moisture provided by intermittent flow and rainfall, and provide an organic substrate for heterotrophic microbial production when surface flow was absent.

Biological sampling and the dynamic ecotone

Stanley et al. (1997) used intermittent desert streams as models to show how changes in flow regime from high to low flow conditions reduce aquatic habitat but increase habitat diversity. Their model of ecosystem expansion and contraction is not limited to desert streams, and should apply equally well to lowland rivers such as the Waipara that are subject to periods of low flow. However, a major challenge to understanding the ecology of expanding and contracting aquatic ecosystems, and hyporheic zones in general (Pugsley & Hynes, 1983; Palmer, 1993; Fraser & Williams, 1997), is sampling their biota. Thus, in

the Waipara, colonisation pots were biased towards sampling larger, typically epigean taxa, such as snails, whereas pump-samples were dominated by minute, non-insect taxa. In addition, pump-sampling and freeze-coring methods rely on the presence of interstitial water to sample the hyporheos, and so are unable to describe changes in the biota of sediments from which interstitial water has receded. In contrast, colonisation-style samplers (e.g. Fraser & Williams, 1997; Hendricks & Rice, 2000), despite their biases, allow for simultaneous measurements of community respiration and invertebrates in the hyporheic zone, are not reliant on saturated interstices to obtain quantitative data, and are therefore suited to sampling across the land-water interface.

Data collected from the Waipara River support contemporary models (Ward, 1989; Vervier et al., 1992; Stanford & Ward, 1993; Stanley et al., 1997; Boulton, 2000) of the hyporheic zone as a spatially and temporally dynamic transition zone between surface water, groundwater and terrestrial ecosystems. My data indicate that the dynamics of the hyporheic zone are strongly influenced by permeability, VHG and the availability of organic matter, which limit the biota temporally, depending on river discharge. Future ecological studies of rivers, groundwater and riparian zones require consideration of the dynamic nature of the hyporheic zone, if the full extent of biological functioning at the juncture of these ecosystems is to be appreciated.

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Chapter 4

Food limitation of hyporheic communities: a field experiment

Introduction

In rivers with extensive riparian vegetation, inputs of leaf litter provide a major source of energy to the aquatic ecosystem. Leaves often accumulate as packs on the substratum surface, forming rich food patches for invertebrate detritivores (Richardson, 1991). Both the feeding of invertebrates on leaves and the activity of microbial decomposers results in the release of nutrients and carbon to other trophic levels and regions of the river (Fazi & Rossi, 2000). Hence, leaf accumulations may have far-reaching effects on river ecosystems.

As well as biological processing of leaves, physical breakdown and movement of detritus play important roles in the supply of organic matter to benthic communities (Young & Huryn, 1997). Large amounts of organic matter is buried within the substratum, particularly during flood events (Naegeli et al., 1995), and may provide "hot spots" of food for microbes and invertebrates. In fact, buried detritus may be considerably more abundant than detritus at the surface (Metzler & Smock, 1990), suggesting that subsurface processing of organic matter may be an important contributor to whole-stream carbon dynamics.

While many experimental studies of litter processing by benthic communities have been made (e.g. Boulton & Boon, 1991; Richardson & Neill, 1991; Quinn et al., 2000b), only a handful of studies have focussed on processing of buried leaves. Rounick & Winterbourn (1983) found lower breakdown and respiration rates and fewer invertebrates on buried *Nothofagus* leaf packs (> 10 cm) than those at the stream surface. In contrast, Smith & Lake (1993) found more invertebrates and more leaf grazing on buried (10 cm) *Eucalyptus* packs than on those at the surface. Boulton & Foster (1998) found no difference in invertebrate community composition between leaf-amended and unamended control sediments at 30 cm depth.

To determine whether community respiration (CR) and invertebrates are food-limited at depth, a field experiment was carried out using colonisation pots. Colonisation pots allowed standardization of substrata and the separation of substrate at different depths. The use of pots with gravel only and plastic leaves as controls allowed for a comparison of the effect of leaves as food versus leaves as habitat provided by leaf addition treatments. I hypothesized that leaf addition would increase CR and invertebrate abundance in proportion to the amount of leaf material added, regardless of depth, due to the high porosity of the substrate. It was also hypothesized that natural leaves would increase invertebrate abundance and CR more than plastic leaves, because of their edibility.

Methods

Study Site

The study site was on the Waipara River, approximately 100 m upstream of Site 7, described in Chapter 3. Mean annual discharge of the Waipara is 2.5 m^3 s^{-1} (Canterbury Regional Council, 1996), although the experiment was undertaken during summer low flow, when discharge was < 1 m^3 s^{-1}. The study reach was a broad (15 m), shallow run (mean depth = 6 cm) dominated by fine gravel and sand. Riparian vegetation was principally willow trees (*Salix* spp.), which provided little shade to the study reach. A previous survey (Chapter 3) had revealed a highly permeable riverbed, with an abundant hyporheic fauna. Water temperature during the experiment averaged 18 °C, and ranged from 13.0 to 26.5 °C.

Experimental treatments

Clean, dry gravel (7-17 mm diameter greywacke sandstone) from a local quarry was placed in 18 hyporheic colonisation pots (9 cm diameter, 45 cm long; described in Chapter 3). Six pots contained gravel only ("control" treatments); six contained gravel with strips of buffed, pre-soaked polythene added ("plastic leaf" treatments) and six had 1 g of air-dried willow (*Salix babylonica*) leaves added per litre of gravel ("willow leaf" treatments). Plastic leaf treatments contained similar shapes and numbers of 'leaves' as the willow leaf

treatments. Willow and plastic leaves were dispersed evenly throughout the depth of pot sediments in the respective treatments.

S. babylonica leaves were chosen as they are palatable to aquatic invertebrates and have been used in numerous benthic leaf litter studies (Pidgeon & Cairns, 1981; Collier & Winterbourn, 1986; Parkyn & Winterbourn, 1997; Schulze & Walker, 1997). Plastic leaves represented a kind of 'habitat control', since natural leaves may be utilized by detritivores for their structural ability to entrain fine particulate matter (Winterbourn, 1978; Richardson, 1992), while other taxa may eat the leaf itself.

Colonisation pots were dug into the Waipara River in early February 2000, and left for four weeks before removal. Four weeks was chosen as a compromise between allowing an adequate period for invertebrate and microbial colonisation (Coleman & Hynes, 1970; Hendricks & Rice, 2000), and for there being sufficient leaf material remaining in the treatments for measurement. A pilot study had shown immeasurably low amounts of leaf organic matter remaining after an incubation period of 7 weeks (unpublished data).

After removal of the gravel-filled basket from each pot, the contents were separated into fractions of 0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm depth, and placed in clean plastic containers. Samples were kept on ice, in the dark, until respiration measurements were ready to be made (< 5 hours).

Respiration of pot sediment (including natural and plastic leaves) and associated organisms was measured in the laboratory in 1.1 litre respirometers made of 90 mm diameter PVC pipe. About 800 ml of sediment from each depth was added to each respirometer which was then filled with Waipara River water at 15 °C. Air bubbles were removed by gentle shaking of the respirometer, and the initial DO concentration of the water was measured to 0.01 mg l^{-1} with a DO meter. Each respirometer was sealed with a press-on cap, to ensure no air gaps remained, and left to incubate on a shaker table in a 15 °C constant-temperature room. DO concentration of the respirometer water was measured after an incubation period of 5 hours by removing the respirometer cap and immediately inserting a DO probe into the water. Community respiration was calculated as milligrams of DO consumed, per litre of sediment, per hour (i.e. mg O_2 litre sediment^{-1} hr^{-1}) after adjusting for DO consumed in a control respirometer containing Waipara River water only.

To compare the contribution of hyporheic (10-40 cm depth) fauna and hyporheic community respiration (CR) to total (0-40 cm depth) fauna and CR, data were expressed in

terms of area rather than volume, assuming a surface area at the top of the colonisation pot of 64 cm^2.

Following the completion of respiration measurements, sediments were washed through a 6 mm mesh sieve onto a 63 μm sieve and preserved in 70% ethanol, to which Rose Bengal had been added to aid the identification of small invertebrates. All invertebrates were sorted under 15-35 x magnification and identified using the keys of Chapman & Lewis (1976) for Crustacea, Winterbourn et al. (2000) for Insecta and Cook (1983) for Acari. To determine ash-free dry mass (AFDM) of organic matter (including added *S. babylonica* leaves), it was elutriated from the inorganic sediment, dried at 50 °C for at least 48 hours, weighed, combusted in a muffle furnace at 400 °C for five hours and reweighed to 0.01 mg.

The water and fine sediment slurry that passed through the 63 μm sieve was kept, and its interstitial silt (< 63 μm) concentration was determined by pipette analysis (Folk, 1965).

Data analyses

To normalize data, invertebrate abundance, silt and AFDM values were log_{10}-transformed. The means of these data were compared among treatment and depth levels using two-way ANCOVA, with silt concentration as the covariate. Post-hoc comparisons of means were made using Tukey tests.

Invertebrate community composition was compared among depths and leaf treatments using non-metric multi-dimensional scaling (MDS), with Sorensen's index as the distance measure (McCune & Mefford, 1999). Axis scores were correlated (Spearman rank) with invertebrate taxa and environmental variables.

Results

Fine sediment, organic matter and community respiration

Interstitial silt concentration averaged 0.71 g per litre of sediment in colonisation pots. Its concentration did not differ between treatments, but a greater amount collected at depths

greater than 10 cm ($F = 2.82$, $P = 0.0487$). On average, 0.42 g of silt collected per litre of pot sediment at 0-10 cm, compared to 0.81 g of silt per litre at 10-40 cm depth (Figure 1a).

The amounts of organic matter (AFDM) collected by plastic leaves and gravel controls did not differ ($P > 0.05$, Tukey post-hoc test). However, the addition of willow leaves resulted in a 9-fold increase in AFDM from 24 mg litre sediment^{-1} in plastic leaf and control treatments to 229 mg litre sediment^{-1} in willow treatments (Figure 1b). In addition, the quantity of organic matter remaining in willow leaf treatments tended to increase with depth ($F = 2.97$, $P = 0.06$, one-way ANOVA, Table 2).

Community respiration (CR) declined with depth, the decline being most marked between 10-20 and 20-30 cm where CR dropped from 0.53 to 0.44 mg O_2 per litre of sediment per hour (Figure 1c). Respiration also differed among treatments, with willow leaves resulting in significantly higher rates of CR than either plastic leaves or controls ($P < 0.05$, Tukey post-hoc test). Plastic leaves increased CR by 13% over controls, while willow leaves increased CR by 35% over controls. When community respiration was expressed per gram AFDM in the willow leaf treatments (Figure 4), a significant decline in respiration was evident with depth ($F = 3.76$, $P = 0.027$).

Invertebrates

The invertebrate community collected in colonisation pots was similar to that collected from other reaches of the Waipara River (see Chapter 3). The fauna was dominated by the hydrobiid snail *Potamopyrgus antipodarum*, which made up 42% of the total fauna (Table 1). Ostracods made up 21% of the fauna, followed by oligochaetes (20%), *Hydora* sp. beetle larvae (7%), and the leptophlebiid mayfly *Deleatidium* sp. (3%). A further 36 taxa contributed to the remaining 7% of the fauna, 14 being insect taxa, and 6 Acari.

Total invertebrate abundance declined with depth ($F = 3.81$, $P = 0.015$), and was 47% greater at 0-20 cm than below 20 cm (Figure 2a). Abundance also differed significantly among treatments ($F = 3.97$, $P = 0.0009$), with plastic leaves increasing abundance by 33% over controls, and willow leaves increasing abundance by 68% over controls. The interstitial silt covariate explained the greatest proportion of variation in the ANCOVA (23%), and was positively related to invertebrate abundance (Table 2).

On average, ten taxa were collected per 0.8 litre of sediment (Figure 2b). Taxon richness was unaffected by depth or interstitial silt, and was slightly, but significantly greater in controls than in plastic or willow leaf treatments ($P < 0.05$, Table 2).

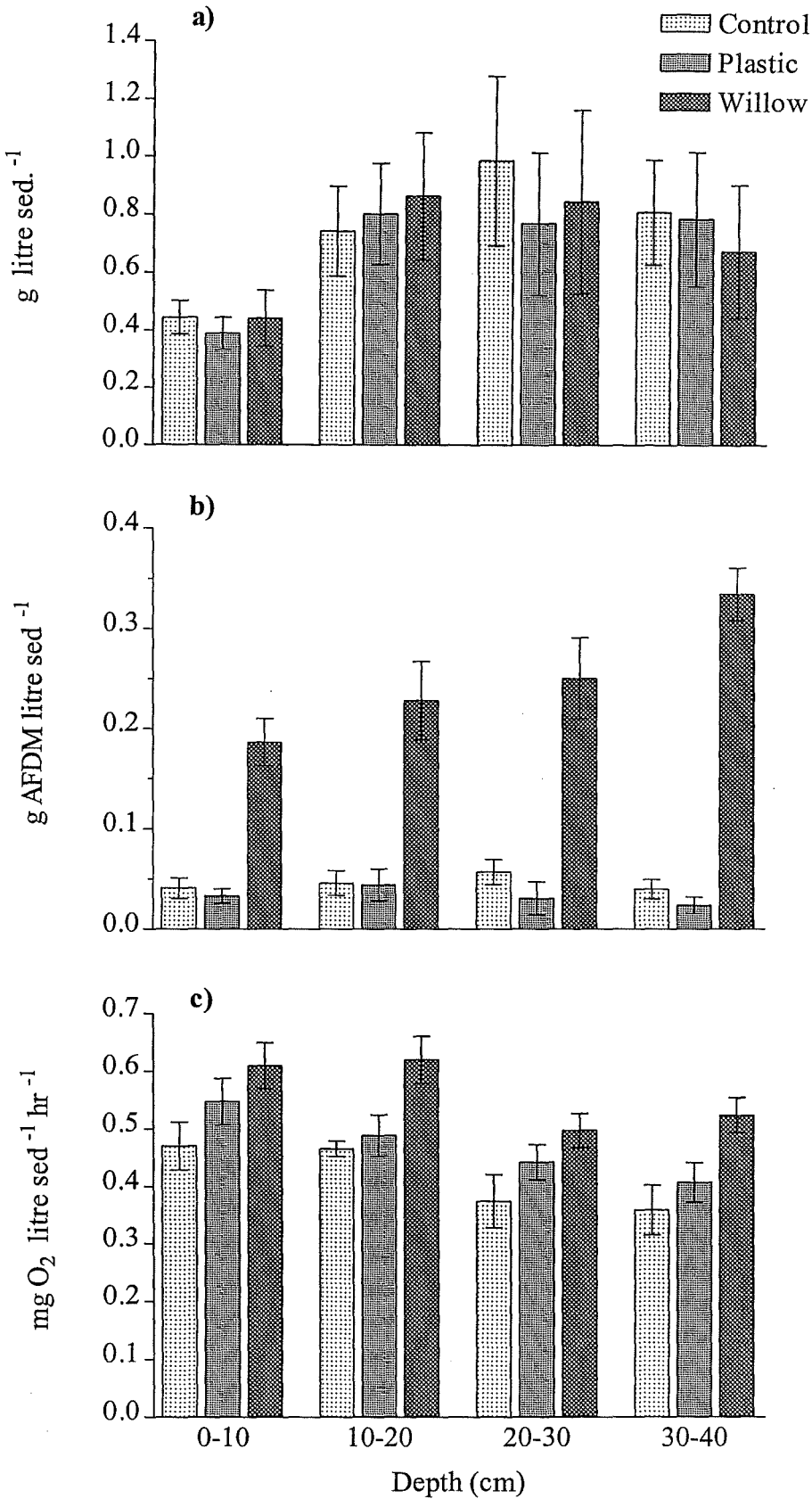

Figure 1. Mean (± 1 SE) a) fine sediment < 63 μm (dry mass), b) AFDM, and c) community respiration per litre of sediment at four depths and in three leaf treatments in colonisation pots after four weeks in the Waipara River.

Table 1. Mean abundance (per litre of sediment) and percentage abundance of the most common taxa collected at 0-40 cm in 68 colonisation pots after four weeks in the Waipara River. Typically surface (epigean) taxa are marked with †.

Taxon	Abundance (No. litre sed^{-1})	Abundance (%)
Potamopyrgus antipodarum (Gastropoda:Hydrobiidae)†	153	41.8
Ostracoda	75	20.5
Oligochaeta	73	20.0
Hydora sp. (Coleoptera: Elmidae)†	26	7.0
Deleatidium sp. (Ephemeroptera: Leptophlebiidae)†	11	3.1
Tanypodinae (Diptera: Chironomidae)†	4	1.2
Tricladida (Turbellaria)	3	0.9
Physa acuta (Gastropoda: Physidae)†	3	0.8
Tardigrada	3	0.7
Hydra sp. (Cnidaria)	2	0.5
Total	353	96.5

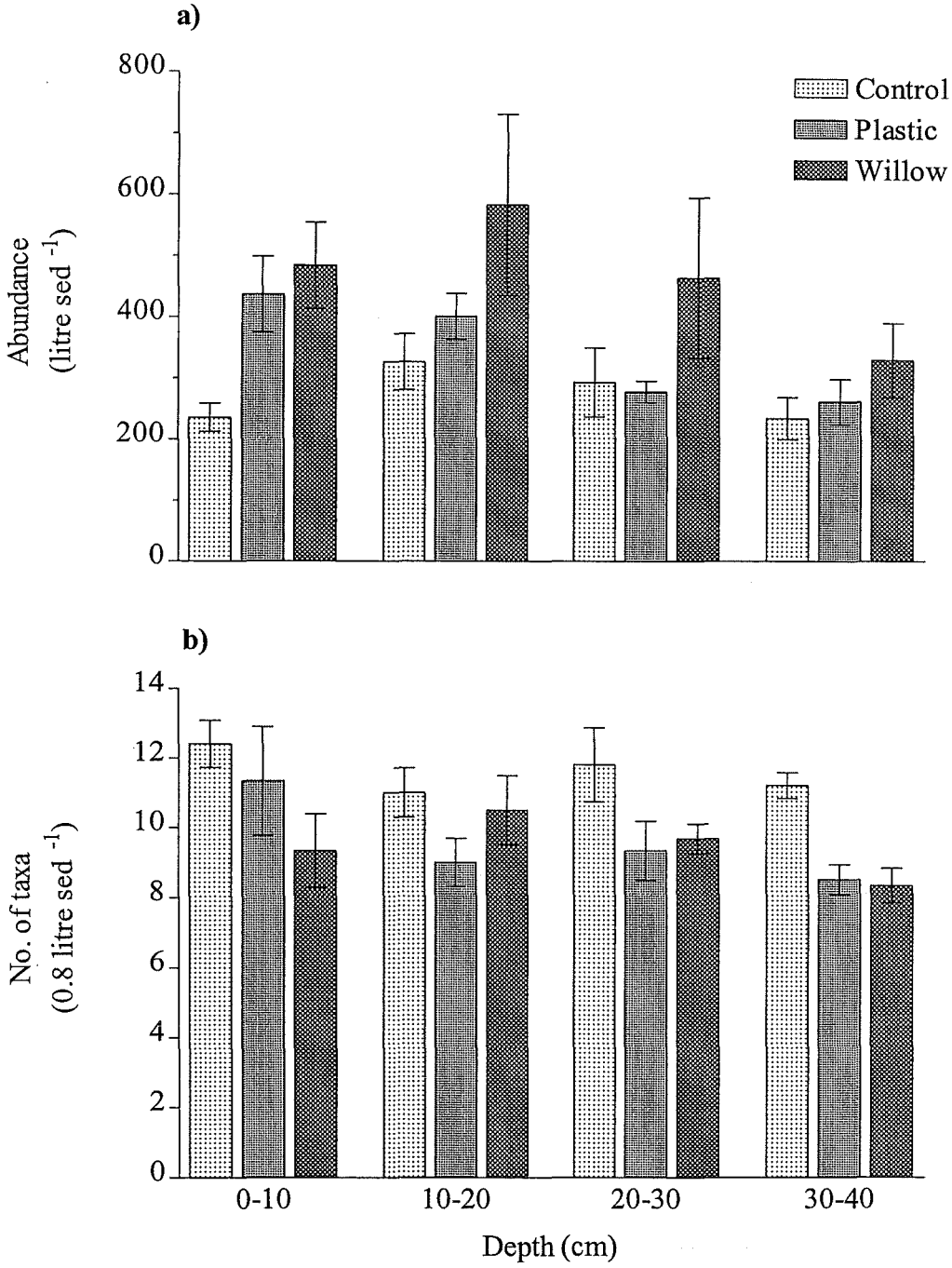

Figure 2. Mean (± 1 SE) a) invertebrate abundance and b) taxon richness in three treatments and at four depths in colonisation pots after four weeks in the Waipara River.

Table 2. Summary of ANCOVA results comparing effects of depth, leaf treatments and interstitial silt content on organic matter (AFDM), community respiration and invertebrate abundance data. Means that do not differ significantly (Tukey $P > 0.05$) are linked by horizontal bars. Abbreviations for depth are: 1 = 0-10 cm, 2 = 10-20 cm, 3 = 30-40 cm, 4 = 40-50 cm. Abreviations for leaf are: C = control, P = plastic leaf, W = willow leaf. Arrows indicate a positive (⇧) or negative (⇩) effect of fine sediment on response variables. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. P-values at, or slightly above 0.05 (i.e. statistical significance) are shown.

Response variable	Covariate			Factors				Contrasts	
	mg silt l^{-1}			Depth		Leaf		Depth	Leaf
	P	r^2	Effect	P	r^2	P	r^2		
AFDM	ns	—	—	0.06	< 1%	***	58%	4 3 2 1	W C P
Respiration	ns	—	—	***	20%	***	27%	1 2 3 4	W P C
Total abundance	***	23%	⇧	***	16%	***	21%	1 2 3 4	W P C
Taxon richness	ns	—	—	ns	7%	**	18%		C P W
Epigean taxa[†]	*	5%	⇩	***	31%	*	7%	1 2 3 4	W P C
Hydora sp.	*	5%	⇩	**	18%	***	17%	2 1 3 4	W P C
Ostracoda	***	47%	⇧	0.05	5%	***	12%		W C P
Oligochaeta	***	53%	⇧	ns	4%	*	4%		W C P
P. antipodarum	***	18%	⇩	*	9%	*	10%	2 1 3 4	P W C
Hydra sp.	**	10%	⇩	ns	< 1%	***	20%		P C W
Deleatidium sp.	ns	—	—	*	15%	ns	4%	2 1 3 4	
P. acuta	ns	—	—	*	7%	ns	3%	1 2 3 4	
Tardigrada	*	9%	⇧	*	14%	ns	2%	1 2 4 3	

[†]Excludes *P. antipodarum*

Of the ten most abundant taxa collected in the Waipara River, the density of five were significantly affected by leaf treatments (Table 2). Two of these taxa and another 3 taxa decreased in density with depth. The abundance of epigean taxa (insects and snails) generally declined with increasing interstitial silt concentration and depth, and differed between treatments. Epigean taxa (insects and molluscs) were 66% more abundant in willow leaf treatments than in gravel controls, while densities were intermediate in plastic leaf treatments (Figure 3). Treatment effects were greatest above 20 cm depth; below this depth, epigean densities declined and treatment differences were less apparent. Ostracods, oligochaetes and tardigrades were positively correlated with interstitial silt concentration, while *Hydora* sp., *P. antipodarum* and *Hydra* sp. were negatively correlated with silt (Table 1). Of these taxa, oligochaetes showed the strongest positive correlation with silt concentration ($r = 0.75$, $P < 0.001$), whereas *P. antipodarum* showed the strongest negative correlation ($r = -0.47$, $P < 0.001$, Figure 5).

Ostracods showed the most dramatic increase in density with willow leaf addition and were three-fold more abundant in willow leaf treatments than in plastic leaf or control treatments (Figure 3). *Hydora* larvae were more abundant in plastic and willow leaf treatments than in controls, while oligochaete density was greatest in willow and lowest in plastic leaf treatments (Figure 3, Table 1). In contrast, *P. antipodarum* and *Hydra* sp. were most abundant in plastic leaf sediments. On average, *P. antipodarum* was 85% more abundant in plastic leaf treatments than in controls, and *Hydra* sp. were 5-6 times more abundant in pots with plastic leaves than willow leaves (Figure 3).

Total invertebrate abundance and community respiration exhibited very similar declines with depth when expressed per gram of organic matter (Figure 4). Community respiration at 30-40 cm was half that at 0-10 and 10-20 cm, and invertebrate abundance declined by 250% over the same depth range. In contrast, ostracod abundance (the second most abundant taxon, and the only group significantly more abundant on willow leaves than plastic leaves) per gram AFDM showed no significant change with depth (Figure 4).

Ordination of invertebrate community samples revealed no obvious trend in composition associated with depth, leaf treatment, or AFDM. However, positive and significant correlations ($P < 0.0001$) were found between axis 2 scores and interstitial silt content ($r_s = 0.78$, Figure 6), and the abundance of oligochaetes ($r_s = 0.84$) and ostracods ($r_s = 0.72$). Community respiration was positively correlated with axis 1 ($r_s = 0.68$, $P < 0.0001$). *P. antipodarum* abundance was also positively correlated with axis 1 ($r_s = 0.64$, $P < 0.0001$), and negatively correlated with axis 2 scores ($r_s = -0.78$, $P < 0.0001$).

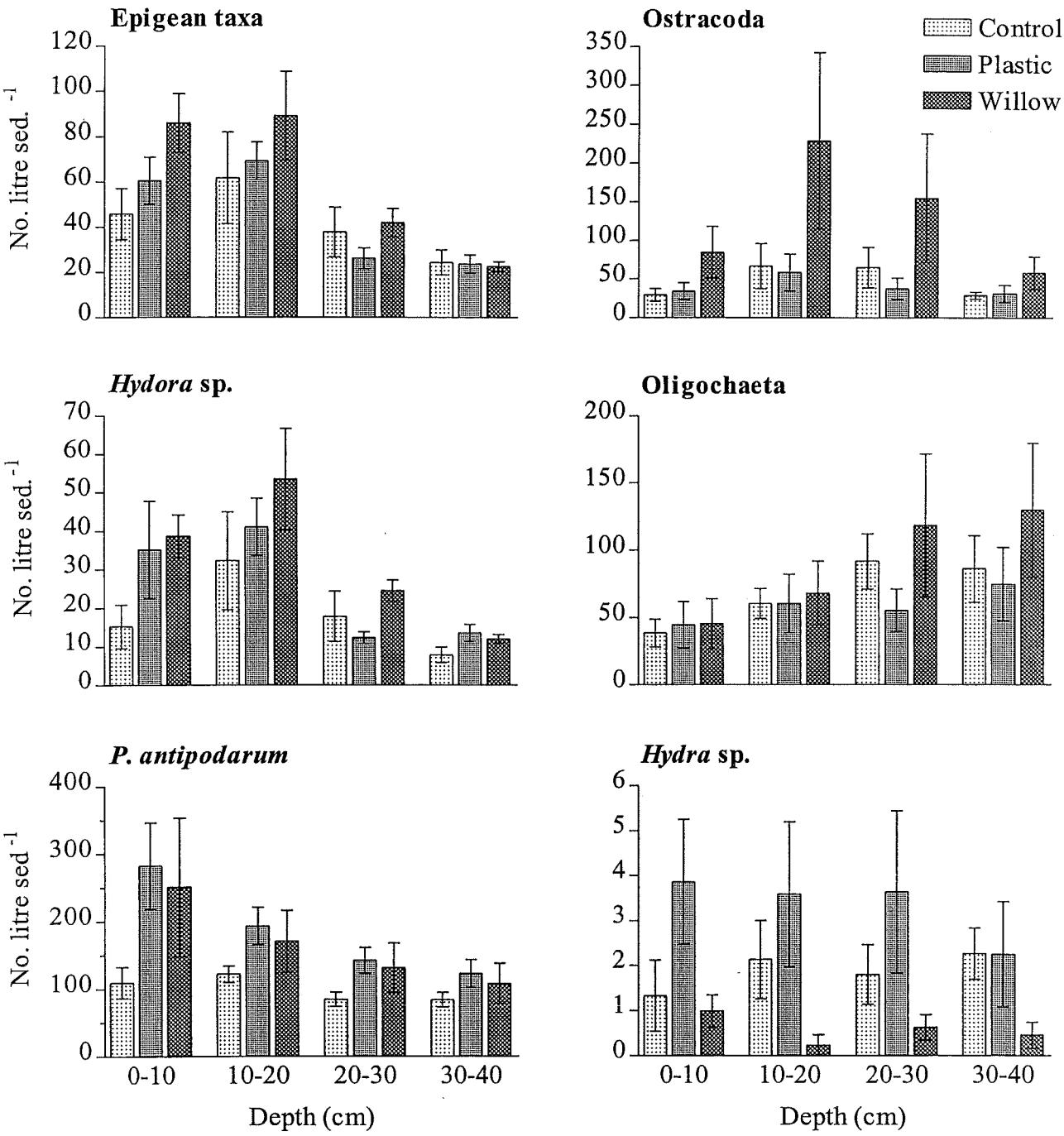

Figure 3. Mean (± 1SE) abundance in colonisation pots of taxa which showed significant differences in abundance ($P < 0.05$, Table 2) among leaf treatments.

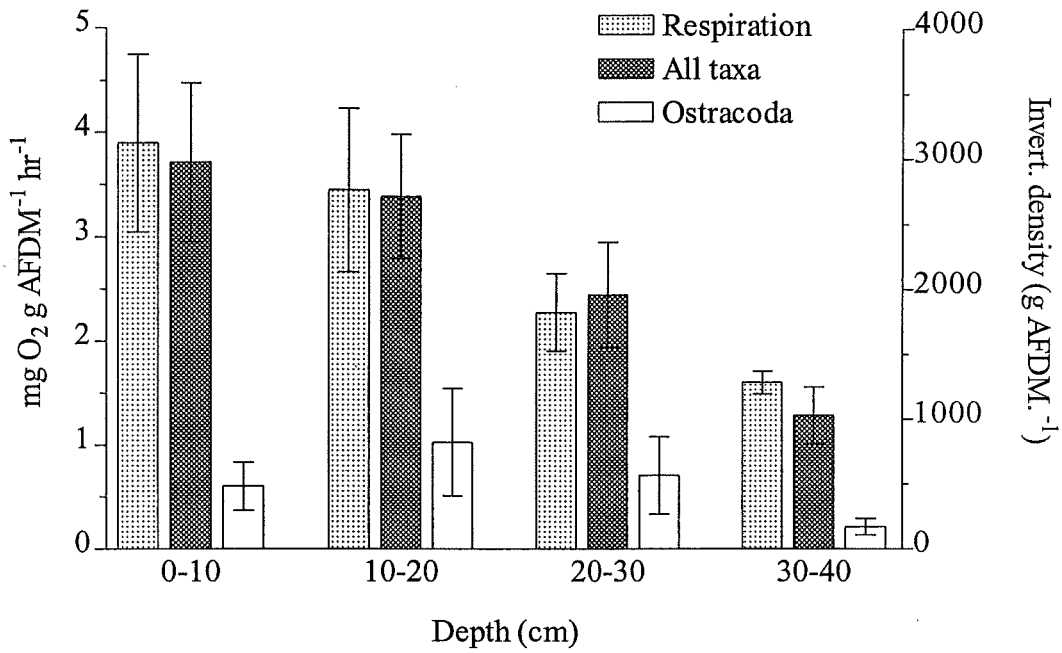

Figure 4. Mean (± 1 SE) abundance of all taxa, Ostracoda, and community respiration, expressed per gram of AFDM in leaf treatments at four depths.

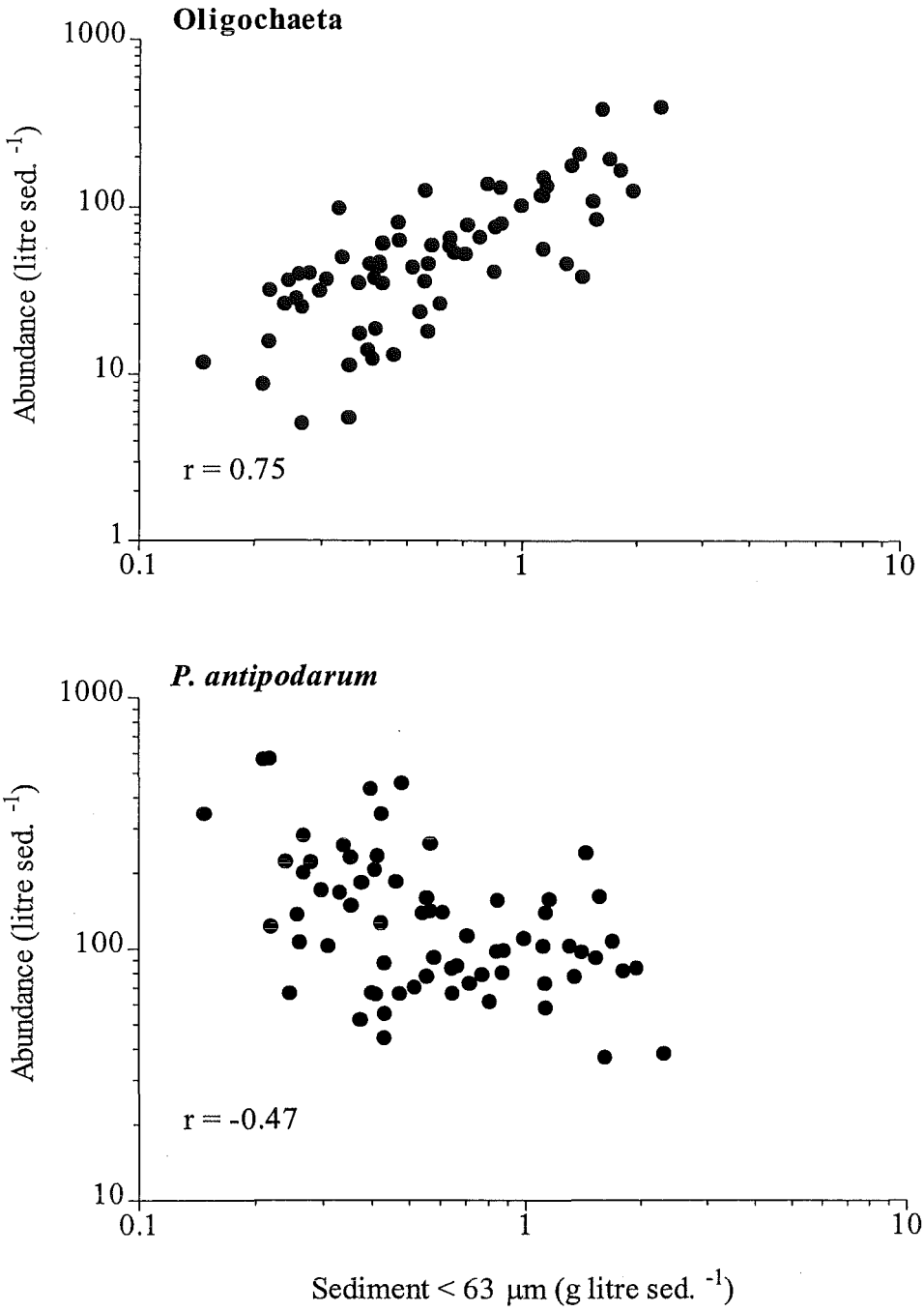

Figure 5. Abundance of oligochaetes and *P. antipodarum* plotted against fine sediment concentration collected at 0-40 cm from colonisation pots in the Waipara River. Correlation coefficients (r) were calculated on $\log_{10}$-transformed data and are statistically significant ($P < 0.0001$). Note logarithmic scales.

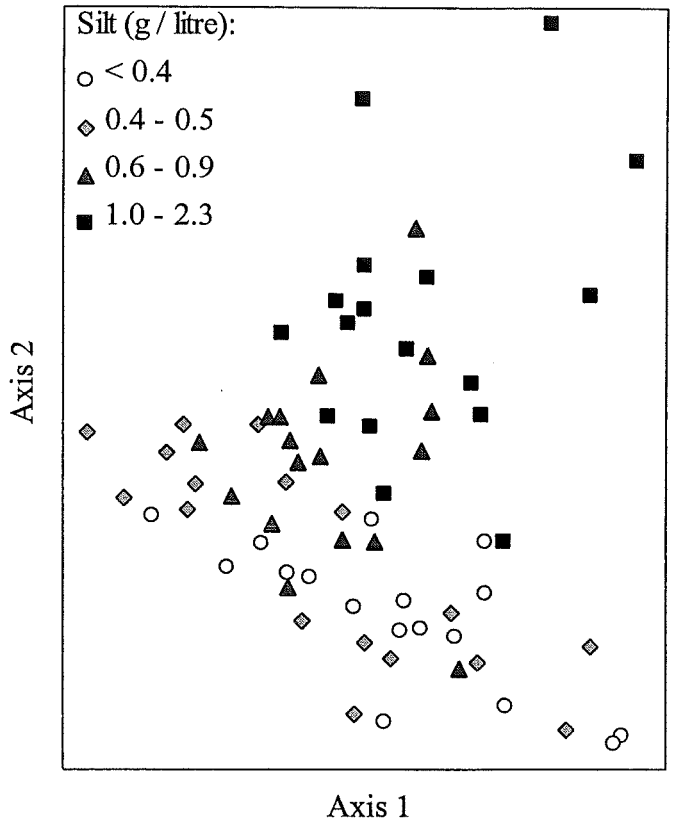

Figure 6. MDS ordination (stress = 0.12) of invertebrate assemblages in colonisation pots after four weeks in the Waipara River. Shading shows fine sediment concentration in pots.

Table 3. The effect of CPOM addition (willow leaves) on mean benthic and hyporheic community respiration and invertebrate abundance, expressed per m^2 of streambed. Values in parentheses are 1 SE.

Treatment	Community Respiration ($g\ O_2\ m^{-2}\ hr^{-1}$)			Invertebrate Abundance (No. m^{-2})		
	Benthic (0-10 cm)	Hyporheic (10-40 cm)	Total (0-40 cm)	Benthic (0-10 cm)	Hyporheic (10-40 cm)	Total (0-40 cm)
Control	0.059	0.151	0.210	29 600	107 400	137 000
	(0.006)	(0.012)	(0.006)	(3 200)	(150)	(17 400)
Leaf	0.077	0.206	0.283	60 800	173 100	233 900
	(0.005)	(0.010)	(0.010)	(8 800)	(42 100)	(54 400)

On average, the hyporheic zone (10-40 cm) contributed 72-78% of total (0-40 cm) invertebrate abundance and CR (Table 3). Benthic (0-10 cm) invertebrate abundance in willow leaf treatments was double that in controls, whereas total (0-40 cm) invertebrate abundance was 72% greater in willow leaf treatments than in controls. CR was 31% and 34% greater in willow treatments than controls in benthic and total sediments, respectively. Willow-amended sediments, including the hyporheic zone, had 7-8 times as many invertebrates and 4-5 times greater CR than benthic sediments with no leaves added (Table 3).

Discussion

The addition of leaves to colonisation pot substrates increased community respiration (CR) and invertebrate abundance in both surface (0-10 cm) and hyporheic (10-40 cm) sediments over gravel-only controls. However, epigean taxa showed no difference in treatment response between artificial leaves and natural leaves. In addition, the stimulatory effect of natural leaf additions on CR and invertebrate abundance declined with depth, although ostracods showed a consistent increase in abundance in the presence of natural leaf litter, regardless of depth.

Leaf breakdown & community respiration

The quantity of leaf fragments remaining in leaf treatments increased with depth, indicating a greater rate of leaf breakdown closer to the sediment surface. Surface-placed leaves also broke down faster than buried leaves in two sand-bottomed streams in North America (Herbst, 1980; Metzler & Smock, 1990), and in two gravel-bed streams in New Zealand (Rounick & Winterbourn, 1983). Mayack et al. (1989) found slower breakdown of buried leaves in a sandy North American stream during winter, but similar rates to surface-placed leaves in spring. Smith & Lake (1993) found no difference in the breakdown rate of surface and buried leaves in an Australian stream in winter.

Leaf breakdown in streams may be due to both physical abrasion and biological processing by microbes and invertebrates (Boulton & Boon, 1991). While physical abrasion and mechanical breakdown of leaves may be considerable at the streambed surface (Campbell et al., 1992; Quinn et al., 2000a), burial reduces the likelihood of

physical abrasion, and may contribute to the slower breakdown of buried leaves (Herbst, 1980). As leaves in the Waipara were effectively protected from physical abrasion at all depths by colonization pots, breakdown was more likely to have been a biological process.

Mayack et al. (1989) and Smith & Lake (1993) attributed similar breakdown rates of surface and buried leaves in their studies to high densities of hyporheic shredders, while anoxia was a likely reason for lower rates of decomposition of buried leaves in two sand-bottomed streams (Herbst, 1980; Metzler & Smock, 1990). Anaerobic conditions were unlikely in either the Waipara or the streams studied by Rounick & Winterbourn (1983), due to high sediment porosity. However, CR per gram of organic matter declined with depth in both studies, suggesting that reduced water exchange may have caused lower oxygen consumption by microbes, resulting in slower decomposition at depth (Rounick & Winterbourn, 1983).

Invertebrates

Invertebrate abundance was stimulated by both artificial leaves and natural leaves, and was greatest on natural leaves. Winterbourn (1978), Richardson (1992), and Quinn et al. (2000b) also found invertebrate abundance was greater on natural leaf packs than artificial leaves. In addition, Richardson (1992), found that high invertebrate abundance (mostly chironomids) in packs of artificial leaves was associated with the fine particulate organic matter they collected. While the amount of organic matter collected in plastic leaf and control treatments did not differ in my study, the surfaces of the artificial leaves (and natural leaves) may have increased the surface area available for microbial colonisation and invertebrate grazing (Smith & Lake, 1993). Slightly greater CR, and a greater abundance of the grazer *P. antipodarum* on plastic leaves than gravel-only controls lend support to this contention.

Ostracods were the only group that was significantly more abundant in the natural leaf-amended pots. Ostracods are often abundant where organic detritus is found, and they feed on it by sweeping small particles into their mouths, or gnawing pieces off larger particles with their mandibular teeth (Delorme, 1991). Copepods and small chironomids preferentially colonised patches of leaves over sandy patches in Goose Creek, Virginia, indicating that small invertebrates are able to discriminate between patches of low and high food quality (Palmer et al., 2000). The accumulation of ostracods in leaf-amended

substrates at all depths in the Waipara pots therefore suggests they may also be able to discriminate between low and high quality patches of food, regardless of depth.

The only other study I am aware of to compare colonisation of buried leaves to unamended sediments was conducted by Boulton & Foster (1998). They found invertebrate abundance and community composition in the hyporheic zone were not related to the presence or absence of added leaves. However, they did find gradients in community composition related to both the direction of vertical hydrologic exchange and interstitial silt content. Boulton & Foster (1998) found greater densities of many taxa, including oligochaetes and small chironomid larvae, in silt-rich samples, whereas samples with less silt harboured a less diverse assemblage. Similarly, the interstitial fauna of the Waipara River showed no change in faunal composition with either depth or food treatment, but the abundance of ostracods and oligochaetes increased in samples containing higher amounts of interstitial silt.

High concentrations of silt can block sediment interstices, increasing the residence time of surface waters, and lowering hyporheic oxygen concentration (Brunke & Gonser, 1997). However, the concentrations of silt in my pots and those of Boulton and Foster (1998) were low, and sediment porosity was high, suggesting that factors other than smothering were responsible for the observed relationships between interstitial silt and community composition. One explanation is that small amounts of silt are advantageous to deposit-feeding invertebrates, such as oligochaetes and ostracods, which are able to ingest it and assimilate the organic portion. These taxa were positively associated with silt concentration and the addition of leaves in the Waipara. In contrast, taxa such as *P. antipodarum* and *Hydora* sp., that predominantly feed by grazing or scraping biofilms associated with solid surfaces, may actively avoid elevated silt concentrations if it interferes with feeding. In the Waipara, *Hydora* sp. and *P. antipodarum* were more abundant in treatments with plastic leaves than gravel controls and were negatively associated with fine sediment. *Hydra* were least abundant in natural leaf treatments, and were negatively associated with silt concentration. Their negative association with organic matter and silt concentration in the Waipara may also have been due to increased fine sediments and FPOM reducing their feeding efficiency as predators.

Waipara data indicate that while some hyporheic taxa, such as ostracods, may respond positively to organic matter enrichment, others appear to respond to relative food quality (inferred from interstitial silt concentration). Numerous studies indicate that stream invertebrates preferentially feed on high quality food at the sediment surface (e.g., Peterson

& Cummins, 1974; Hanlon, 1981; Parkyn & Winterbourn, 1997; Quinn et al., 2000b), however relatively few studies have associated food quality with invertebrate abundance in the hyporheic zone. In the Töss River, Switzerland, Brunke & Gonser (1999) found a strong positive association between the ratio of POM to total fine particles and hyporheic invertebrate abundance. In addition, they found a closer relationship between this measure of POM *quality* and invertebrate abundance than POM *quantity* and invertebrate abundance. In the Speed River, Canada, Lenting & Williams (1997) also attributed greater invertebrate abundance and taxon richness on buried maple leaves than cedar leaves to the high carbohydrate content of the former, a measure of their potential food value.

Application of experimental results

A drawback to conducting hyporheic experiments is the need to disturb the surrounding substrate in order to manipulate variables at depth (Palmer, 1993). Also, the use of standardised substrate in colonisation pots may poorly represent naturally heterogeneous hyporheic substrate and hydrologic flowpaths, and may be biased towards sampling epigean taxa (Palmer, 1993; Fraser & Williams, 1997; Hendricks & Rice, 2000). Despite these drawbacks, colonisation pots enabled the response of the interstitial community to leaf addition to be compared to unammended controls at different depths in the substrate. My results therefore provide experimental support for the positive associations between hyporheic POM content and invertebrate abundance and microbial activity in my field surveys (Chapter 2) and those of Metzler & Smock (1990), Pusch & Schwoerbel (1994), Naegeli et al (1995), and Brunke (1999).

Data from the Waipara River and elsewhere (e.g., Williams & Hynes, 1974; Grimm & Fisher, 1984; Marchant, 1988; Pusch & Schwoerbel, 1994; Naegeli et al., 1995; Fuss & Smock, 1996; Adkins & Winterbourn, 1999; Fellows et al., 2001) indicate that the hyporheic zone can make a substantial contribution to whole-stream metabolism and invertebrate production. In my experiment, the addition of leaves and inclusion of hyporheic sediments to a depth of 45 cm increased areal estimates of invertebrate abundance 7-fold, and community respiration 4-fold over estimates for benthic sediments (0-10 cm) with no leaves added. From these results, it is clear that the hyporheic zone can be an important region of organic matter processing, and should be included in models of river ecosystem carbon dynamics.

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Chapter 5

Growth of *Olinga feredayi* (Trichoptera: Conoesucidae) on surface and hyporheic foods

Introduction

An abundant and diverse invertebrate fauna lives below the surface of the streambed. This fauna is composed of taxa that are typically subsurface-dwelling ("permanent hyporheos"), but also includes groups that are more commonly found at the sediment surface (epigean taxa, or the "occasional hyporheos", sensu Williams & Hynes, 1974). A large number of crustacean taxa often dominate the permanent hyporheos (e.g. Bretschko & Leichtfried, 1988; Palmer, 1990), many of which show adaptations to the subsurface environment. These adaptations include an ability to withstand low dissolved oxygen (DO) concentrations, and possession of a low metabolic rate (Malard & Hervant, 1999). In contrast, typical epigean taxa include a number of insect groups (Williams & Hynes, 1974), which usually require a highly oxygenated environment, and must emerge from the stream as adults to complete their life cycles.

Why epigean taxa are found deep in stream sediments has been the subject of much speculation. A popular hypothesis is that the hyporheic zone presents a refuge from disturbances such as drought (Clinton et al., 1996; del Rosario & Resh, 2000) or flooding (Palmer et al., 1992; Dole-Olivier et al., 1997; Gayraud et al., 2000). It has also been suggested that the hyporheic zone represents a biological refuge from competition or predation at the sediment surface (Wagner, 1990; Adkins & Winterbourn, 1999). Hyporheic invertebrates may also ingest biofilms and particulate organic matter (POM), in the hyporheic zone (Boulton, 2000). In general, however, the ecology of hyporheic invertebrates is poorly understood, and little experimental research has been undertaken on their ecological requirements.

Several studies have found a positive correlation between organic matter content and invertebrate abundance in the hyporheic zone (Pusch, 1996; Strayer et al., 1997; Brunke & Gonser, 1999). In addition, Franken et al. (2001) suggested that hyporheic

invertebrates may be attracted primarily to biofilms, and that their positive associations with detritus may be due to richer biofilm development on detritus than on inorganic particles.

Rounick & Winterbourn (1983) found several invertebrate taxa were able to assimilate components of heterotrophic biofilms grown in the dark, and suggested that the lower surfaces of stones, and subsurface sediments are likely to be grazed by invertebrates. However, Blenkinsopp et al. (1991) found more cellular energy storage products in light-grown biofilms than those grown in the dark, and suggested that the upper surfaces of stones would provide more energy per unit area to invertebrate grazers. Bärlocher & Murdoch (1989) found that gut extracts of the eipigean *Tipula caloptera* (Diptera) and hypogean *Gammarus tigrinus* (Amphipoda) contained enzymes capable of releasing amino acids from proteins and carbohydrates of hyporheic biofilms. However, it remains unclear whether dark-grown or hyporheic food sources are sufficient to sustain invertebrate growth.

O. feredayi (Conoesucidae) is a very common, widely distributed New Zealand caddisfly, which constructs smooth cases made entirely of tanned secreted protein (Cowley, 1978). Larvae feed on dead leaves, fine particulate organic matter (FPOM) and biofilms (Cowley, 1978; Lester et al., 1994; Winterbourn, 1982; Quinn et al., 2000; Winterbourn, 2000), and both Huryn (1996) and Scarsbrook (1995) found larvae at depths of up to 45 cm below the streambed surface in Otago Streams. Similarly, Adkins & Winterbourn (1999) found 40-60% of larvae below 10 cm in 30 cm cores taken from two alpine streams in the central South Island. I found similar proportions of *O. feredayi* at depths of 0-15 cm and 15-30 cm in substrate-filled colonisation tubes in the Glentui River (Figure 1), where the work reported here was undertaken.

In this chapter, the ability of *Olinga feredayi* to grow on food sources from surface (light and dark) and hyporheic environments was investigated. The aim was to determine whether this member of the occasional hyporheos can grow equally well on potential food sources (biofilm and POM) found in surface and subsurface environments. I predicted that dark and hyporheic biofilms would be less abundant and of poorer quality than light biofilms, and would result in lower growth of *O. feredayi* grazing on them.

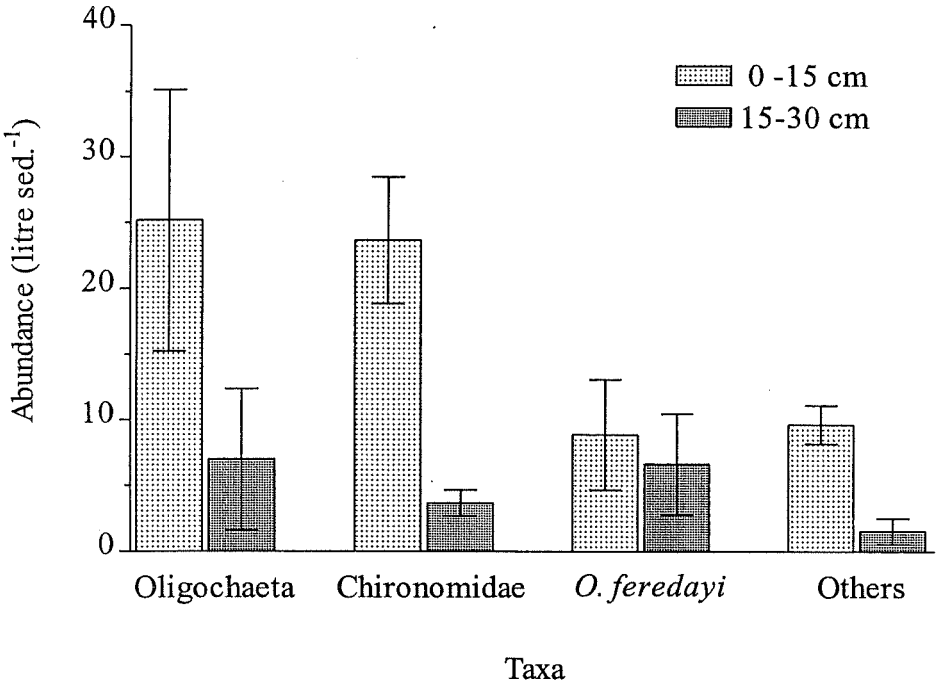

Figure 1. Mean abundance (± 1 SE) of common taxa collected in colonisation pots taken from the Glentui River in July 1998, after an 8 week colonisation period.

Methods

Study Area

The Glentui River is a tributary of the Ashley River in the eastern foothills of the Southern Alps. The headwaters of the Glentui River are in mountain beech (*Nothofagus solandri* Hook) forest, but the study site was in a lower section of the river (172° 18', 43° 14'), where a mixture of native broadleaf trees (predominantly *Coriaria arborea* and *Coprosma* spp.) and willows (*Salix* sp.) occurred in the riparian zone. The river at the study site (upper Glentui reach, Chapter 2) was 2.9-4.4 m wide and 8-16 cm deep at baseflow. Surface sediments were mostly loosely packed pebbles and cobbles (8-64 mm diameter). The experiment was conducted during summer baseflow when discharge did not vary greatly, and averaged about 30 l s^{-1}. Earlier studies in the Glentui River reported a diverse and abundant benthic invertebrate fauna dominated by insect larvae (Cadwallader, 1975; Devonport & Winterbourn, 1976). Hyporheic taxa include oligochaetes, chironomids and *O. feredayi* (Figure 1).

Experimental Design

The growth of *O. feredayi* was investigated in laboratory mesocosms, which consisted of 750 ml plastic containers with a 90 mm diameter base. The bottom of each container was covered with aquarium gravel (median diameter 4 mm), filled with stream water (Glentui River) and aerated. Mesocosms were maintained at 15 °C in a constant temperature room, with a light cycle of 12 hours light and 12 hours dark.

Each mesocosm contained a single larva and one of the following food treatments:

1. Control (= no cobble)
2. Light grown biofilm
3. Dark grown biofilm
4. Hyporheic grown biofilm
5. Hyporheic grown biofilm + fine particulate organic matter (FPOM)
6. Dark grown biofilm + FPOM
7. Light grown biofilm + FPOM
8. Light grown biofilm + leaves (CPOM)

Fifteen replicates of each treatment were established for a total of 120 mesocosms. Water and food were renewed weekly, and the inner surface of the container was scrubbed to remove unwanted biofilm growth.

Hyporheic biofilms were grown on cobbles incubated in plastic mesh bags in hyporheic colonisation pots. The bags of cobbles were held in colonisation pots 15-30 cm below the streambed, with a second bag of stones above them to fill the pot. Cobbles were left in the pots for 6 weeks prior to the grazing experiment, to allow hyporheic biofilm to develop (Pusch & Schwoerbel, 1994; Ellis et al., 1998). Dark-grown biofilms were obtained by placing cobbles in plastic mesh cages covered by non-transparent perspex for 6 weeks. Light-grown biofilms were those naturally occurring on the upper surfaces of cobbles collected from the surface of the streambed, in vicinity of the colonisation pots.

FPOM was collected from the colonisation pots. As numerous minute invertebrates were associated with it and could not be removed readily, the FPOM was blended on high for 30 second, to kill them. CPOM was represented by leaves of *Coriaria arborea* collected from Wooded Gully Stream, a nearby tributary of the Ashley River. All larvae of *O. feredayi* used in experiments also came from Wooded Gully Stream.

One biofilm-covered cobble was placed in each 750 ml container, and about 20 ml of the FPOM suspension was added to each of the biofilm+FPOM treatments. Case length of each larva was measured to 0.1 mm with a graticule in the eyepiece of a dissecting microscope. At the start of the trial they ranged from 5.3-8.2 mm.

The experiment ran for 40 days, when the case lengths of all larvae were remeasured. Individuals were removed from their cases, dried (70 °C for 3 days), and weighed (to 0.01 mg) on a Cahn microbalance. Mean growth per food treatment was reported as both change in case length, and change in body mass. Initial weights were interpolated from the power equation below, which is based on body mass and case length measurements of 40 larvae collected from Wooded Gully Stream:

$$\ln(\text{mg body mass}) = 3.1493 \times (\ln(\text{mm case length})) - 6.084 \quad (r^2 = 0.86)$$

To obtain a measure of larval "condition" (sensu Baker, 1989), the mass of individuals at the end of the experiment was subtracted from the mass predicted by the mass-length equation. Because I suspected that hyporheic larvae may be in poorer condition than those at the surface, the relationship between case length and body mass was determined also for

40 *O. feredayi* larvae collected from the hyporheic zone (20-30 cm) and 40 from the surface sediments of another Canterbury river (Okuti River).

Biofilm measurements

Two weeks prior to the end of the experiment, seven cobbles were removed from each of the biofilm treatments (light, dark and hyporheic). The surface area of one face of each cobble was scrubbed (the upper surface in the case of the "light" cobbles) in 60 ml of stream water. The scrubbings were kept cool in the dark until processing began (less than 4 hours). The surface area scrubbed was estimated by tracing the outline of the stone onto sheet plastic, cutting it out and comparing its weight with that of a plastic square of known surface area.

Biofilm ash-free dry mass (AFDM) was determined by filtering 20 ml of biofilm scrubbings through precombusted glass fibre filters (Whatman GF/C). Filters were then dried at 50°C for 24 hours and combusted at 450 °C for five hours. Further 20 ml aliquots of the biofilm scrubbing were passed though precombusted GF/C filters for the determination of chlorophyll *a* concentration. Filters were placed in 90% ethanol and extracted at 4°C in the dark overnight. The absorbance of chlorophyll *a* was measured at 665 nm, following correction for turbidity at 750 nm, on a Uvikon 860 (Kontron Instruments) spectrophotometer, and expressed per unit area (Jespersen & Christoffersen, 1987). The remaining slurry was preserved with a few drops of 100% formalin and 200 µl was pipetted onto a black polycarbonate filter (0.2 µm pore size). The filtered sample was stained with 100 µl of DAPI in the dark for 2 hours. Following staining, the number of bacterial cells, fungal hyphae and POM were counted in three fields of view, at 400 x magnification, using a fluorescent light source (Porter & Feig, 1980; Ledger & Hildrew, 1998).

Subsamples of preserved biofilm were also used for algal counts and identification. Algal units were counted with a haemocytometer, at 400 x magnification. An algal unit was a diatom or green coccoid cell or a green filament (Ledger & Hildrew, 1998). The number of fields of view counted per sampled varied (50-150), depending on algal density. Diatoms were identified to genera (Foged, 1979), whereas filamentous green algae and coccoid green algae were not identified further.

Faecal pellets that collected in vials while the larvae awaited measurement were combined within replicates of each of the light, dark, and hyporheic biofilm treatments. The relative abundance of diatoms, fungal hyphae, bacteria, inorganic material (silt), and POM in the pellets was compared among the treatments using epifluorescence microscopy, following staining with DAPI. Three fields of view were scanned per treatment.

Data analyses

To achieve normality prior to statistical testing, measures of larval growth were $\log_e$-transformed, whereas AFDM, chlorophyll *a* concentration and microbial counts were $\log_{10}$-transformed. One-way ANOVA was used to test the effect of the different food treatments on the growth of *O. feredayi*. ANOVA was also used to compare the individual biofilm descriptors (AFDM, chlorophyll *a*, and microbial counts) among the light, dark and hyporheic biofims. Following a significant ANOVA, pairwise comparisons of means were made using Tukey tests. Associations among biofilm descriptors were examined by calculating Spearman rank correlation coefficients.

Results

Biofilm Composition

Chlorophyll-*a* concentration was greatest in the light treatment (mean = 0.52 μg cm^{-2}) , and was significantly lower (Tukey test, $P < 0.001$) in both the dark and hyporheic treatments (means = 0.02 and 0.01 μg cm^{-2}, respectively), (Figure 2). AFDM was greatest in the light treatment (147 μg cm^{-2}) and was 4-6 times lower in the dark and hyporheic treatments (Tukey, $P < 0.001$, Figure 2).

Bacteria were the most abundant microbial component of biofilms in all light treatments (Figure 3). The density of bacteria ranged from 1.7 x 10^6 cells cm^{-2} (light treatment) to 2.2 x 10^6 cells cm^{-2} (dark treatment), but did not differ statistically (ANOVA $F = 0.99$, $P = 0.39$) among treatments.

The abundance of fungi differed significantly (Tukey, $P < 0.05$) between all biofilm types (Figure 3). The density of fungal hyphae in the light treatment was 4.7 x 10^5 cm^{-2},

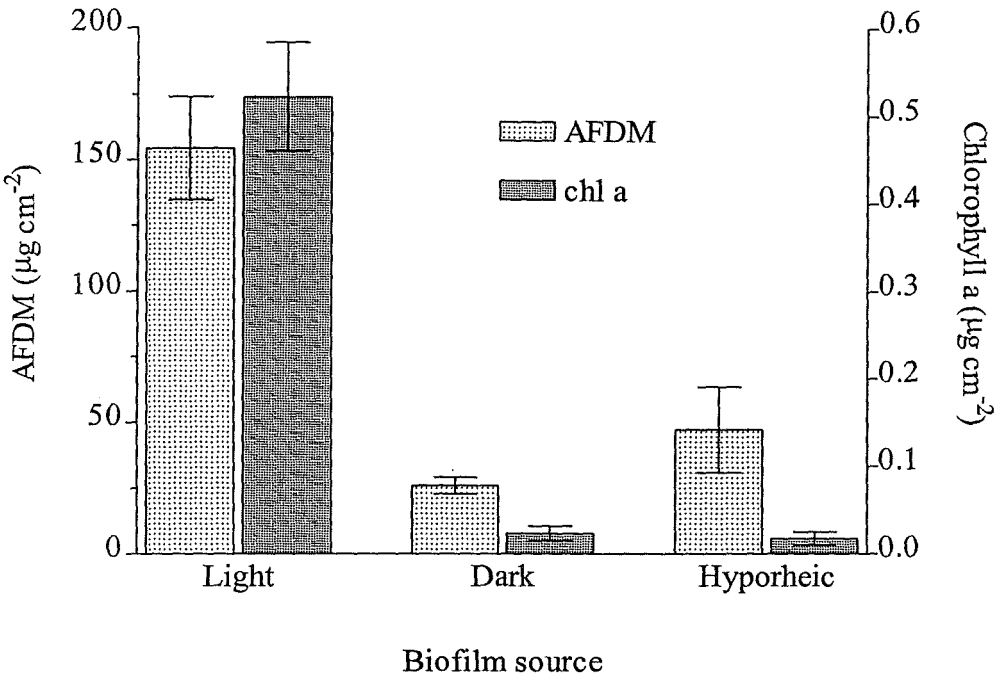

Figure 2. Mean (± 1 SE) mass of chlorophyll *a* and AFDM in biofilms grown on cobbles incubated in the Glentui River under different light treatments.

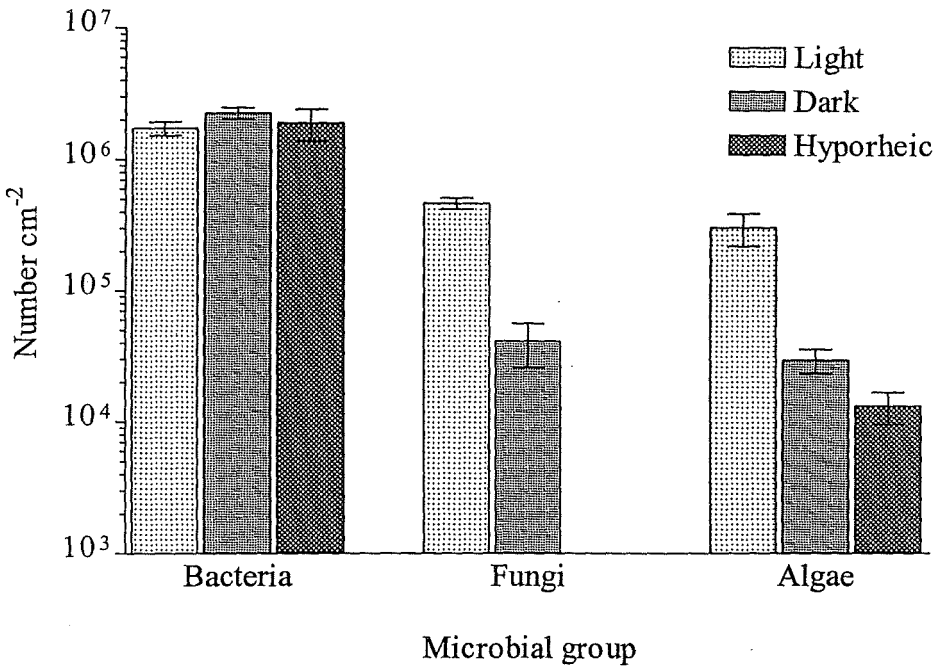

Figure 3. Mean (± 1 SE) abundance of bacteria, algal units, and fungal hyphae collected from biofilms grown on cobbles in the Glentui under different light treatments.

whereas an order of magnitude fewer fungal hyphae were found in the dark treatment (8.6×10^4). No fungal hyphae were detected in hyporheic biofilms.

Dark biofilms contained significantly fewer algae than light biofilms (Tukey, $P < 0.01$), but algal density in dark and hyporheic biofilms did not differ significantly (Tukey, $P = 0.22$, Figure 3). Mean density of algal units in biofilms decreased from 2.5×10^5 cm^{-2} in light biofilms to 2.4×10^4 cm^{-2} in dark biofilms and 3.5×10^3 cm^{-2} in hyporheic biofilms. While some algae were present in hyporheic biofilm samples, they were not seen in others, despite scanning 150 haemocytometer fields.

Bacterial cell density was not correlated with AFDM, or any other biofilm measures. In contrast, abundances of both algae and fungal hyphae were significantly and positively correlated with AFDM ($r_s = 0.76$ and 0.66, respectively, $P < 0.001$), and each other ($r_s = 0.77$, $P < 0.0001$). Chlorophyll-*a* and AFDM were also positively correlated ($r_s = 0.69$, $P < 0.001$), but the ratio of chlorophyll-*a* to AFDM declined from light to hyporheic treatments, as algal abundance was reduced.

Algal composition

Ten diatom taxa were identified in the samples, five of which were only found in the light treatments. Unicellular, coccoid green algae and the stalked diatom *Gomphonema* were the most common algae in the light biofilms (Figure 4). *Cocconeis*, *Navicula*, and *Gomphonema* were the most abundant genera in the dark treatments. The only algal taxa found in hyporheic biofilms were adnate diatoms, *Navicula* being the most common, followed by *Cocconeis* and *Cymbella*.

Gut contents

Examination of faecal pellets voided by *O. feredayi* larvae at the end of the experiment showed differences in food egested (and by inference ingested) that reflected the food sources to which larvae had been exposed (Figure 5). Fungal hyphae comprised 48% of faecal material of larvae supplied with light biofilms. Bacteria were most abundant in faecal pellets of larvae from dark biofilm treatments (66%), while larvae in hyporheic biofilm treatments had a greater proportion of detritus (51%). Diatoms contributed 17-20% of faecal pellets of larvae from all three light treatments.

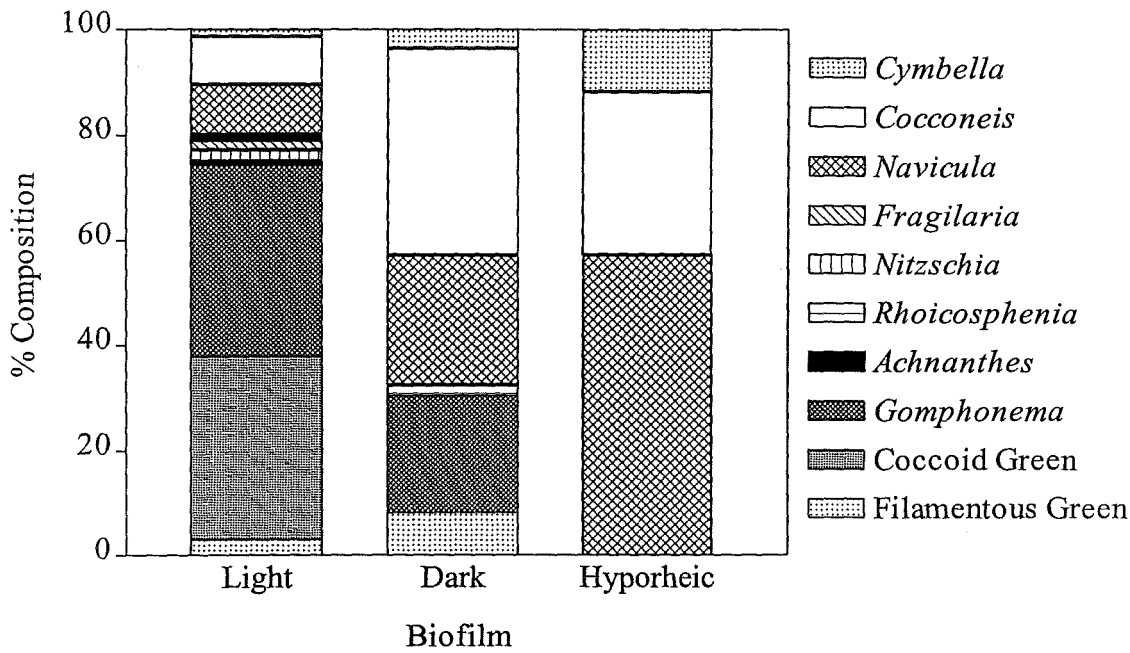

Figure 4. Percentage composition of the most abundant algal groups in biofilms grown under different light conditions in the Glentui River.

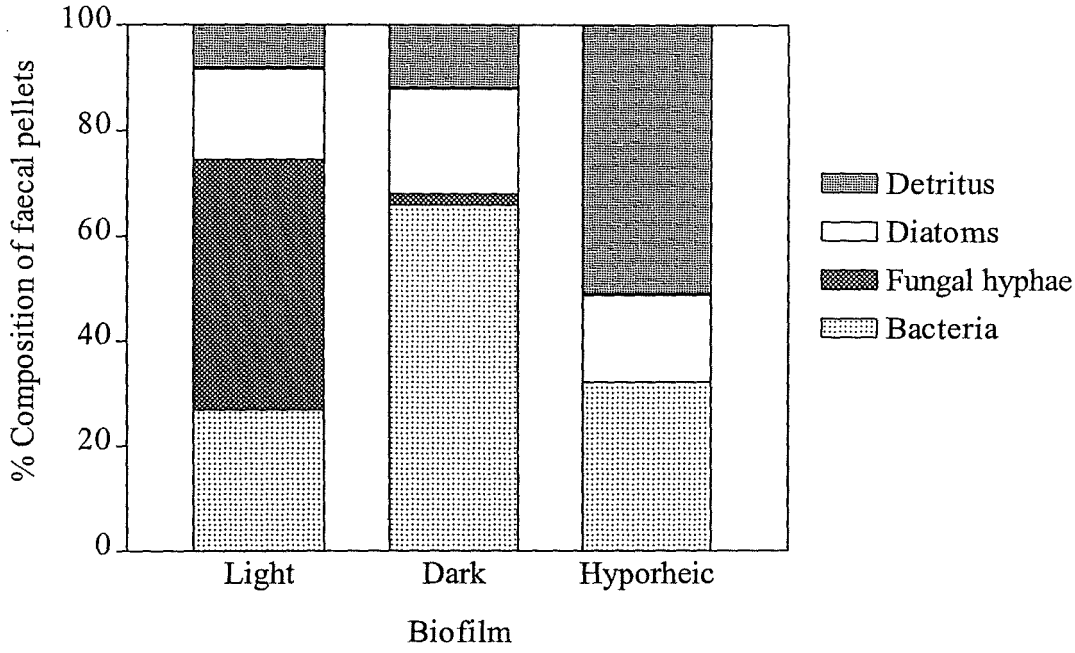

Figure 5. The composition of faecal pellets voided by *O. feredayi* larvae fed different food types (n=3).

Larval growth

Survivorship of larvae was high in all experimental treatments, with 99 of the 105 individuals (94%) surviving the 40 day experiment. However, larvae showed negative, or no growth on many of the food sources supplied (Figure 6). In some mesocosms, larvae were observed outside their cases, cutting off the anterior ends of them. Larvae did not appear to be ingesting their cases, since some excised "rings" of case material were found in the mesocosms. *O. feredayi* cases became shorter over the length of the experiment in the control, hyporheic and dark treatments, whereas those in the light treatment and the FPOM-amended hyporheic and dark treatments showed no change in length. Larvae only extended their cases in the light biofilm treatments amended with FPOM or CPOM.

Weight differences between the start and end of the experiment showed similar trends to the case length data, with larvae gaining mass only in the light biofilm with FPOM and CPOM treatments (Figure 6). However, differences in larval growth expressed as change in length and change in mass prompted a comparison of final mass predicted by the mass-length regression, and actual mass of weighed larvae. Overall, a weaker relationship was found between the predicted and observed mass of larvae in control or biofilm-only treatments than in the biofilm treatments with FPOM or CPOM, indicated by differences in their coefficients of determination (Figure 7). The biofilm treatments with FPOM and CPOM also had significantly higher slopes ($F = 10.67$, $P = 0.002$) than biofilm-only and control treatments, suggesting that larvae supplied with particulate organic matter were in better 'condition'.

Larvae supplied with leaves and light biofilm had a condition factor of 1 (Figure 8), indicating that their body mass-case length relationship was the same as those of larvae taken from Wooded Gully Stream. In contrast, condition scores of larvae from all other treatments were lower (means 0.6 – 0.9), and the condition of those fed light, dark and hyporheic biofilms was significantly lower than those fed light biofilm with FPOM or CPOM (Tukey, $P < 0.05$).

The relationship between case length and body mass of *O. feredayi* larvae collected from the hyporheic zone and surface sediments was identical ($F = 1.22$, $P = 0.27$, Figure 9), indicating no difference in condition between hyporheic and surface-collected larvae.

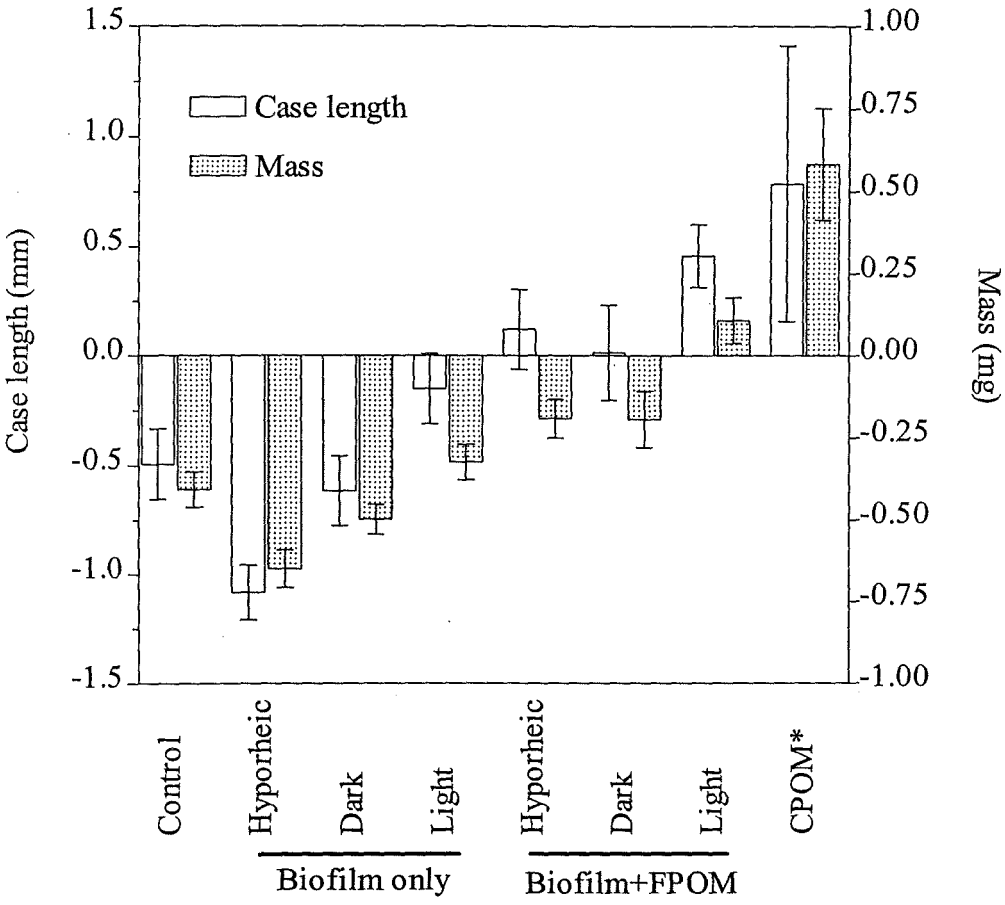

Figure 6. Mean (± 1 SE) change in case length and dry mass (excluding case) of *Olinga feredayi* larvae fed various combinations of biofilm and POM for 40 days. * The CPOM treatment contained leaves and light-grown biofilm.

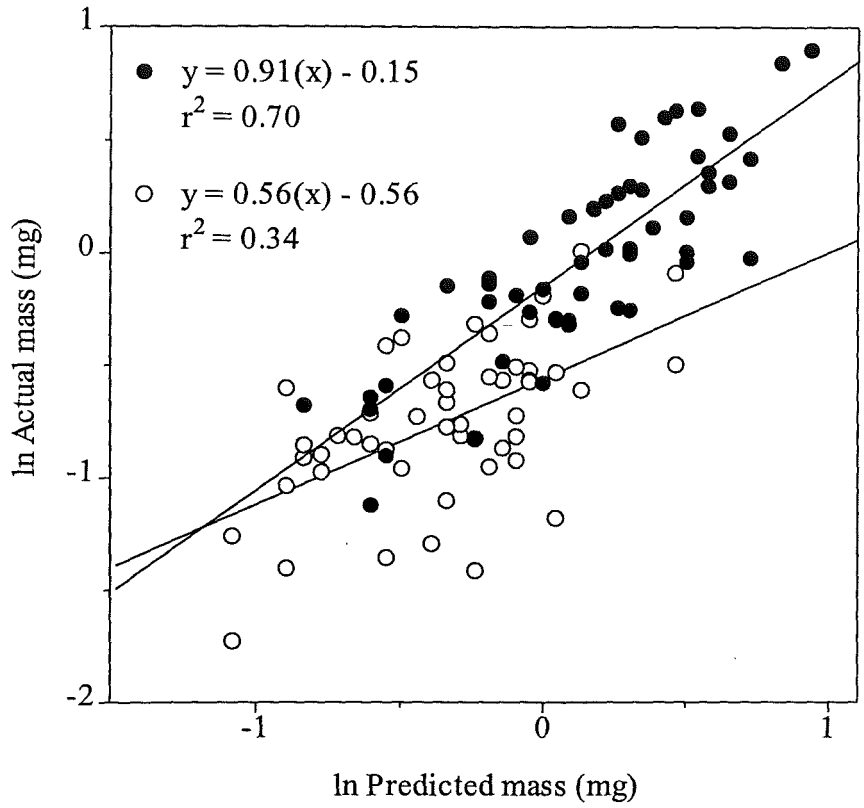

Figure 7. The relationship between predicted mass (based on case length-mass regression) and actual mass of *Olinga feredayi* larvae fed surface and hyporheic foods for 40 days. Open circles = biofilm and control treatments; closed circles = biofilm with FPOM and CPOM treatments.

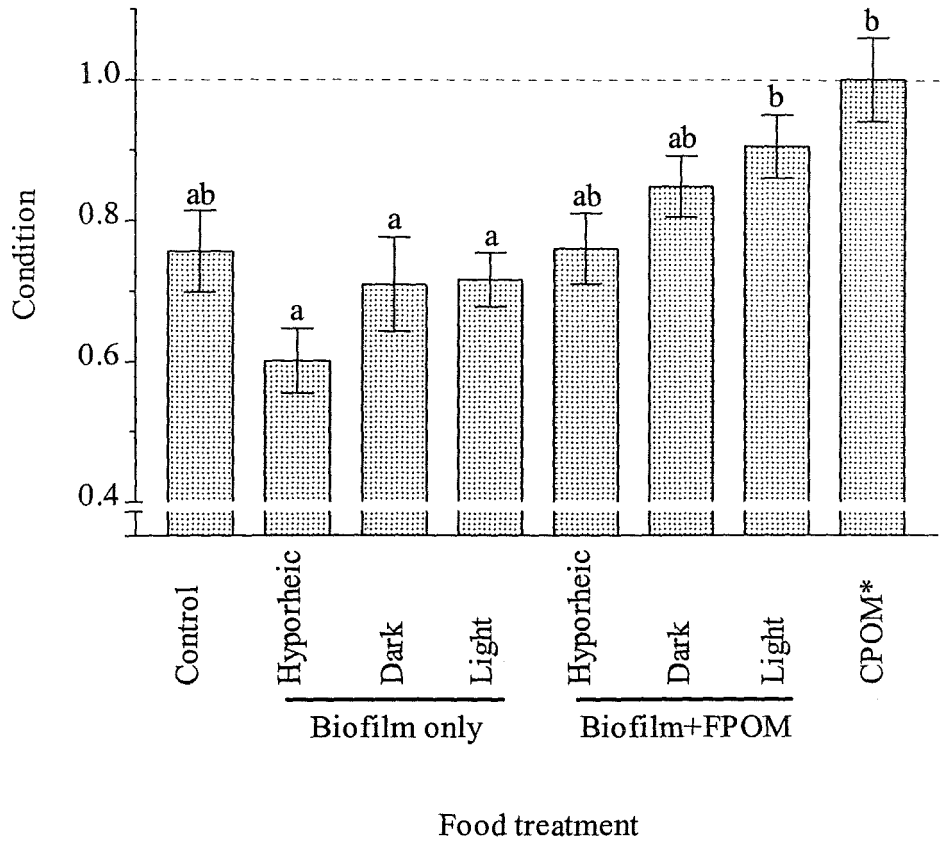

Figure 8. Mean condition (± 1 SE) of *O. feredayi* larvae fed various diets in the laboratory. * The CPOM treatment contained leaves and light-grown biofilm. Means sharing the same superscript letter are not significantly different (Tukey test, $P < 0.05$).

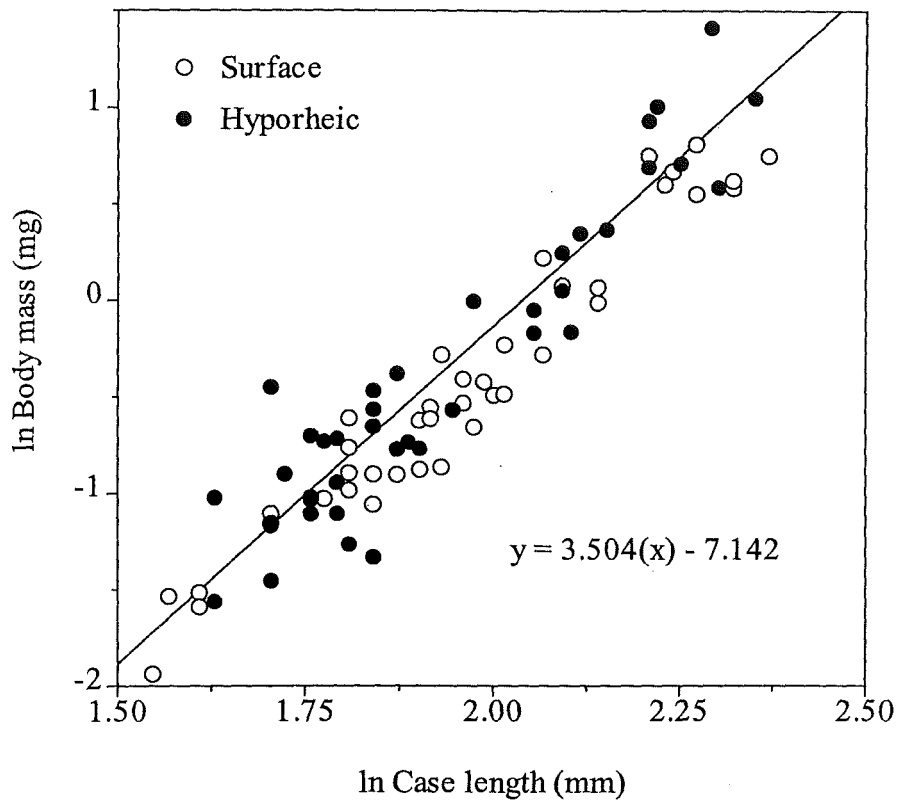

Figure 9. The relationship between case length and body mass for *O. feredayi* larvae collected from the sediment surface (n = 40) and 20-30 cm below the surface in hyporheic colonisation pots (n = 40). The slopes and intercepts of the two regression lines are the same.

Discussion

Light, dark and hyporheic epilithon

The greatest difference in microbial community composition was found between light and dark (including hyporheic) biofilms. Dark biofilms had significantly less AFDM, chlorophyll *a*, fungal abundance and algal diversity than light biofilms. Light biofilms were dominated by green algae and the diatom *Gomphonema*, whereas dark and hyporheic biofilms had higher proportions of *Navicula* and *Cocconeis*. In two Canadian rivers, Lock et al. (1984) also found *Cocconeis* on the underside of stones, and *Gomphonema* on upper surfaces in the light. Similarly, Ellis et al. (1998) found common river diatoms (including *Synedra*, *Achnanthes*, *Navicula*, *Gomphonema*, *Cocconeis*, and *Cymbella*) and green algae in floodplain wells over 2 km from the active channel of the Flathead River, Montana, although chlorophyll *a* concentrations were only 2-3 % of that in the active channel.

The high abundance of fungi in light-grown biofilms was unexpected, since they are often absent from sun-exposed surfaces (Bärlocher & Murdoch, 1989), and are most commonly associated with organic substrates (Wong et al., 1998). A close relationship between algae and bacterial cells in streams has been noted by several authors (Geesey et al., 1978; Rounick & Winterbourn, 1983; Ledger & Hildrew, 1998), who suggest that epilithic bacteria use algal exudates for nutrition. The abundance of algae and bacteria were not correlated in this study, however, a close correlation between the abundance of algae and fungi was found and may imply a link between algal and fungal production. Some aquatic hyphomycetes are known to take up dissolved organic matter (DOM) (Maltby, 1996), and the fungi in my light-grown biofilms therefore may absorb algal exudates.

No fungal hyphae were found in hyporheic biofilms, but Barlocher & Murdoch (1989) found they contributed 2% of total microbial biomass of hyporheic epilithon in a Canadian stream. Ellis and Stanford (1998) found fungi were abundant in floodplain wells hydrologically connected to the Flathead River, but were uncommon in the river and in wells immediately adjacent to it. The ecology of fungi in the hyporheic zone is poorly understood, although it seems likely that their abundance in the hyporheic zone is limited by the availability of POM and dissolved oxygen (Findlay & Sobczak, 2000).

Larval growth

Rounick & Winterbourn (1983) found a number of common stream invertebrates were able to feed on and assimilate thin biofilms grown in the dark in two montane streams in New Zealand. I also found that *O. feredayi* ingested light, dark and hyporheic biofilms, however growth of larvae occurred only when light-grown biofilm supplemented with either FPOM or CPOM was provided. Light biofilms contained a greater abundance of algae and fungi than the dark and hyporheic biofilms. Epilithic algae are regarded as a high quality food resource for invertebrate grazers (Lamberti, 1996), and fungi also may be a nutritious source of food for invertebrate grazers and shredders (Arsuffi & Suberkropp, 1986; Wong et al., 1998). In addition, Blenkinsopp et al. (1991) found that biofilms grown in well-lit conditions contained a higher concentration of energy storage products (glycogen and poly-beta-hydroxyalkanoate) than those grown in the dark, and suggested that the upper surfaces of stones would therefore provide the greatest calorific gain to invertebrate grazers.

Bärlocher & Murdoch (1989) found that biofilms from the hyporheic zone (10 cm depth) of a Canadian stream contained both bacteria and fungi. These biofilms released amino acids and sugars when exposed to gut extracts from *Gammarus tigrinus* and *Tipula caloptera*, indicating that they contained potentially nutritious proteins and carbohydrates. Bärlocher & Murdoch (1989) therefore suggested that some invertebrates might move to regions within the hyporheic zone where the epilithon was particularly well developed or nutritious. Several studies (Lester et al., 1994; Parkyn & Winterbourn, 1997; Quinn et al., 2000) have found that *O. feredayi* prefers and grows better on high quality foods, such as well-conditioned, soft leaves, than on leaves of less nutritional value (higher C:N or phenolic content) or periphyton. Larvae of the European caddisfly *Sericostoma personatum* burrow into the substrate during the day, but feed on CPOM at the substrate surface at night and will not feed on buried leaves (Wagner, 1991). My laboratory observations indicate that *O. feredayi* are also nocturnally active, highly mobile, and therefore may have a similar foraging pattern to *S. personatum*. Alternatively, *O. feredayi* may move between high and low quality resource patches in the hyporheic zone, and at the substrate surface. In the Waipara River, ostracods preferentially colonised hyporheic substrates supplemented with willow leaves over unamended sediments (Chapter 4), supporting the contention that some members of the hyporheos are able to discern between patches of high and low food quality.

Larval mortality was very low (6%) during the 40 day feeding experiment. This indicates that as well as being an ideal organism for laboratory feeding studies, *O. feredayi* can survive for sustained periods in the absence of high quality food. This may also explain why they can be abundant in the hyporheic zone, where food appears to be of poor quality, and may be patchily distributed.

Mass-length regressions are commonly used to predict the dry mass of benthic insect larvae, despite considerable variability in their precision (Johnston & Cunjak, 1999). Nevertheless, Towers et al. (1994) found a very strong relationship between case length and body mass of *O. feredayi* (r^2 = 96%). However, in the present study I found that the mass-length relationship was affected by food quality. Under-matching of predicted mass by actual body mass was due to poorer larval "condition"; whereby "starved" larvae (offered biofilm only) weighed less per mm of body length than well-fed larvae (offered light biofilm with POM). Comparable differences in invertebrate condition and biomass of damselflies were also associated with food limitation (1989), whereas pH, and water temperature were implicated by Griffith et al (1993) and Short et al (1987) in studies of stoneflies and dobsonflies, respectively.

As well as losing condition, poorly fed larvae shortened their cases when fed poor quality food. The large oeconesid caddisfly *Zelandopsyche ingens* also shortened its case when poor quality food was provided (Winterbourn & Davis, 1976), however, larvae used the microbially colonised case material (small twigs and leaf fragments) as food (Winterbourn & Davis, 1976). In contrast, the case of *O. feredayi* is made entirely of tanned secreted protein (Cowley, 1978), is very tough and unlikely to be digestible. A large amount of energy must be expended by larvae in constructing these thick cases (Otto & Svensson, 1980), and this, coupled with the increased susceptibiliy to predation of larvae when outside their cases (Otto & Johansson, 1995), makes case-shortening an energetically-expensive, and potentially risky exercise. However, the greater energy expended in carrying around a case that has become too large or ill-fitting for a larva in poor condition, may prompt it to shorten its case. Thus, case shortening by *O. feredayi* may be a conservative, energy-efficient response to food limitation.

In summary, the epilithic microbial community found in the shallow hyporheic zone of a New Zealand stream was similar to that of heavily-shaded epilithon, and both had less biomass and less diverse microbiota than epilithon grown in full light. While the epigean caddisfly *O. feredayi* ingested hyporheic foods, it did not grow in the absence of either higher quality light-grown epilithon, or POM. These results suggest that epigean

invertebrates should only be found in the hyporheic zone when either food resources are sufficiently great enough for growth, or (as in the case of *O. feredayi*) when they can move readily between resource patches in the hyporheic zone and at the substrate surface.

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Chapter 6

Fine sediment effects on hyporheic communities: a field experiment

Introduction

Benthic invertebrates show affinities for mineral substrata of different sizes, often preferring coarse substrates to fine (Pennak & Van Gerpen, 1947; Cummins & Lauff, 1968; Rabeni & Minshall, 1977; Williams & Mundie, 1978; Angradi, 1999). Substrate particle size varies naturally in rivers, depending on local geology, but may also become drastically reduced when human activities such as farming (Harding & Winterbourn, 1995; Quinn et al., 1997), forestry (Campbell & Doeg, 1989) and mining (Quinn et al., 1992) introduce high concentrations of fine sediment into waterways (Wood & Armitage, 1997). Suspended sediment increases turbidity, reducing light penetration and algal production (Van Nieuwenhuyse & LaPierriere, 1986; Davies-Colley et al., 1992) and may increase invertebrate drift (Rosenberg & Wiens, 1978; Doeg & Milledge, 1991; Suren & Jowett, 2001). Deposited fine sediment may reduce epilithic food quality to invertebrate grazers (Ryder, 1989; Graham, 1990; Quinn et al., 1992), bury invertebrates (Dobson, 2000; Runde & Hellenthal, 2000) and block sediment interstices, reducing the permeability of the substrate to solutes, microbes and invertebrates (Brunke & Gonser, 1997).

The hyporheic zone represents the transition between surface water and groundwater (Orghidan, 1959), and its fauna and microbiota can contribute greatly to overall stream metabolism (Pusch, 1996; Mulholland et al., 1997; Fellows et al., 2001). The hyporheic zone is likely to be sensitive to sedimentation, since fine sediments reduce hydraulic conductivity, increase the residence time of hyporheic water, and result in lowered interstitial dissolved oxygen concentrations (Rutherford et al., 1995; Dodds et al., 1996). The effect of fine sediment on interstitial dissolved oxygen is more likely to affect the biological community than the reduction in interstitial space per se (Jansson, 1967), although finer sediments may filter-out particulate organic matter, resulting in indirect limitation of carbon in the hyporheic zone (Chafiq et al., 1999; Brunke & Gonser, 1999).

Angradi (1999) found lower interstitial flow rates, and lower benthic invertebrate abundance and diversity in Appalachian stream sediments with high concentrations of interstitial fines (< 2 mm diameter), while Richards & Bacon (1994) found a negative correlation between the abundance of sediment 180-850 μm diameter and invertebrate abundance and taxon richness in the hyporheic zone of Bear Valley Creek, Idaho. Increased sedimentation was implicated also as a reason for low interstitial dissolved oxygen and low invertebrate diversity and abundance in some New Zealand pasture streams (Boulton et al., 1997).

The aim of the study reported in this chapter was to compare how the surface and hyporheic communities of a lowland Canterbury river respond to manipulated concentrations of fine sediment < 2 mm diameter. I hypothesized that epigean invertebrates (typical surface fauna) would be more strongly affected by high concentrations of interstitial fines than hypogean species that spend their entire lives in the interstitial environment. I also predicted that while microbial activity (as indicated by cotton decomposition potential) may be stimulated by low concentrations of interstitial fine sediment, due to an increase in surface area for colonisation (Jones, 1995; Alfrieder et al., 1997), it would be negatively affected by high concentrations of fine sediment, due to reduced sediment porosity and interstitial flow.

Methods

Study Site

My study site was on the Waipara River, approximately 55 km north of Christchurch. Mean annual discharge of the Waipara is 2.5 $m^3 s^{-1}$ (Canterbury Regional Council, 1996), although the experiment was undertaken during summer low flow, when discharge was < 1 $m^3 s^{-1}$. The study reach was approximately 100 m upstream of Site 7, Chapter 3, in a broad, shallow run (mean depth = 5 cm) dominated by fine gravel and sand. Riparian vegetation was principally willow trees (*Salix* spp.), which provided little shade to the study reach. Water temperature during the experiment averaged 18.4 °C, and ranged from 12.0 – 26.0 °C.

Experimental design

Clean, dry gravel (7-17 mm diameter greywacke sandstone) from a local quarry was placed in 24 hyporheic colonisation pots. Pots were 11 cm diameter and 45 cm deep, and composed of a PVC frame covered in 8 mm plastic mesh (further details are given in Chapter 3). Six pots contained gravel only ("control" treatments) and the remaining 18 contained varying concentrations of fine sediment. Fine sediment, hereafter referred to as "fines", consisted of crusher dust, sand, clay and silt, collected from a local quarry, and had been dry-sieved through a 2 mm mesh screen. Fines were added to pot gravels so that the percentage of total sediment dry weight consisting of fines was 5%, 15%, and 45%. A small amount of water was added to each of the fine sediment and gravel mixtures, to enable the fines to be mixed evenly through the gravel, and to minimise "shake-down" of fines during transport. Six replicate pots representing each of the three fine sediment treatments were established.

Colonisation pots were dug into the Waipara River in early January, 2000, and left for four weeks before removal. After removal of the gravel-filled basket from each tube, the contents were separated into fractions of 0-15 cm, 15-30 cm and 30-45 cm depth and placed in clean plastic containers with associated interstitial water. Samples were kept cool (ca 5 °C) on ice, in the dark, until respiration measurements were made (< 5 hours).

Microbial activity

Cellulose decomposition potential was measured using the cotton strip assay (Harrison et al., 1988). The cotton strip assay has been used widely to measure cellulose decomposition potential in soils (Harrison et al., 1988), and has proven useful in several freshwater studies (Hildrew et al., 1984; Boulton & Quinn, 2000). For details of the method see Boulton & Quinn (2000). Briefly, strips of standard Shirley Soil Burial Test Fabric (60 mm warp, 20 mm weft) were autoclaved, and inserted horizontally into colonisation pot sediments, one each at 7, 23 and 37 cm depth, prior to pot burial in the field. After four weeks in the river, strips were removed from the sediments immediately prior to the measurement of sediment respiration, rinsed with distilled water and dried at room temperature. Six additional strips served as controls, which received the same handling as test strips but were not buried long enough (< 60 minutes) for microbial decomposition to occur. Control strips were processed as for test strips. Cotton strips

were kept at 25°C and 65% relative humidity for 24 hours the day before testing, as recommended by Howson (1988). The tensile strength of all strips was measured to the nearest 0.001 kilo-Newton (kN) on a tensometer. The tensile strength of each treatment replicate was deducted from the mean tensile strength of the controls and reported as cotton tensile strength loss (CTSL), in kN. The number of days taken for 50% loss of tensile strength to occur (CT50) was determined using the formula of Hill et al (1985):

$$CT50 = t / (CTSL / y)^{0.33}$$

where t is the incubation period (in days) and y is the final tensile strength of the test strip.

Respiration of pot sediment and associated organisms was measured in the laboratory in 1.1 litre respirometers made of 90 mm diameter PVC pipe closed at one end. About one litre of packed sediment was added to each respirometer which was then filled with Waipara River water at 15 °C. Air bubbles were removed by gentle shaking of the respirometer, and the initial dissolved oxygen (DO) concentration of the water was measured to 0.01 mg l^{-1} with a YSI DO meter and probe. Each respirometer was sealed with a press-on cap, to ensure no air gaps remained, and left to incubate on a shaker table in a 15°C constant-temperature room. DO concentration of the respirometer water was measured after an incubation period of 5 hours by removing the respirometer cap and immediately inserting a DO probe into the water. Community respiration was calculated as milligrams of DO consumed per litre of sediment per hour, after adjusting for DO consumed in a control respirometer containing Waipara River water only.

Sediment & invertebrate sorting

Following the completion of respiration measurements, sediments were washed through a 6 mm screen onto a 63 μm mesh sieve. The water and sediment slurry that passed through the 63 μm sieve was kept and the mass of silt (2 – 62 μm) and clay (< 2 μm) was quantified using pipette analysis (Folk, 1965). Sediments and biota retained on the 63 μm sieve were preserved in 70% ethanol, to which Rose Bengal had been added to aid the identification of small invertebrates. Prior to sorting, sediments and invertebrates were rinsed through a series of nested sieves with 2 mm, 1 mm, and 0.5 mm openings, and retained on a 63 μm mesh sieve. All invertebrates were sorted under 15-35 x

magnification and identified using the keys of Chapman & Lewis (1976) for Crustacea, Winterbourn et al. (2000) for Insecta and Cook (1983) for Acari.

The proportions of total fauna made up of insects and epigean (insects and snails) taxa were calculated as metrics potentially sensitive to high concentrations of fine sediment. To test whether fine sediment affected macro- and meiofauna differently, the proportion of total invertebrates and insects that were meiofauna was determined. Meiofauna were defined as animals that passed through a 500 μm sieve and were retained on a 63 μm sieve.

Following removal of invertebrates, all sediments and associated organic matter were dried at 60°C for at least 48 hours, weighed to 0.1 mg, ashed in a muffle furnace at 400°C for five hours and reweighed to determine ash-free dry mass (AFDM). The ratio of AFDM to dry weight of fine particles < 2mm (AFDM/TFP) was calculated as a measure of food quality (Brunke & Gonser, 1999). The higher the organic fraction the greater the assumed food value to invertebrates.

To estimate the porosity of substrate samples, variable amounts of fines (0-25%) were added to gravels in the laboratory. Porosity of the sediments was determined using the formula of Freeze & Cherry (1979):

$$\text{Porosity} = 100 \times (1 - P_b / P_c)$$

where P_b (bulk mass density) is the oven-dried weight of the sample divided by its field volume, and P_c (particle mass density) is the oven-dried mass of the sample divided by the volume of solid particles, as determined by a water displacement test.

Data analyses

To normalise data, AFDM/TFP, respiration, CTSL, and invertebrate abundance data were $\log_{10}$ - transformed prior to analysis, and percent fines and percent invertebrate abundance data were arcsine-transformed.

Grain size analysis of sediment samples indicated a high degree of overlap of fine sediment concentrations among treatments. For this reason, the effect of depth and fine sediment concentration on invertebrate abundance was tested using ANCOVA, with depth as a factor, and fine sediment as a covariate, rather than as a categorical variable. As part

of the ANCOVA, regression slopes relating invertebrate abundance to fine sediment concentration were computed and compared among depths, allowing the interactive effects of depth and fine sediment on invertebrate abundance to be tested. ANCOVA was used also to relate depth and fine sediment to AFDM, community respiration and CTSL.

Invertebrate community composition was ordinated using non-metric multidimensional scaling (MDS) on PC-ORD (McCune & Mefford, 1999), with Sorensen's index as the distance matrix (Faith et al., 1987). To help interpret the ordinations, axis scores were correlated (Spearman rank) with invertebrate abundance and fine sediment percentage data.

Results

Sediment characteristics

The mean concentration of fine sediment < 2 mm in pot samples was 7% (127 g l^{-1}), and ranged from 0.3 – 23% (5 – 554 g l^{-1}) of total sediment dry weight. On average, sand (0.063 – 2 mm) made up 6.5% (115 g l^{-1}) of sediment weight (Figure 1), while silt and clay (< 0.063 mm) made up only 0.6% (12 g l^{-1}). Although the concentration of fines did not differ significantly among depths ($F = 2.5$, $P = 0.09$), the range of fine sediment was greatest among 30-45 cm depth samples (0.6 - 23% fines < 2 mm) and least in the 0-15 cm samples (0.3 - 14%) (Figure 1).

Porosity showed a negative linear relationship with increasing interstitial fines (Figure 2). Porosity ranged from 35% for gravels with no fines added, to 17% in a sample including 24% fines.

The dry weight of sediment organic matter (AFDM) collected in pots after four weeks declined with depth and was positively associated with the concentration of fines ($r^2 = 0.70$, $P < 0.001$, Figure 3a). AFDM responded more positively to increased fine sediment at depths < 15 cm than at depths > 15 cm, as indicated by the different slopes of the sediment versus AFDM regression lines for these depths (ANCOVA depth x sediment interaction, $P < 0.05$, Figure 3a).

The contribution of organic matter mass to total fine particulate mass < 2 mm diameter (AFDM/TFP) was negatively correlated with the concentration of fines ($r^2 = 0.73$, $P < 0.001$) and did not decline with depth (Figure 3b). However, AFDM/TFP was more

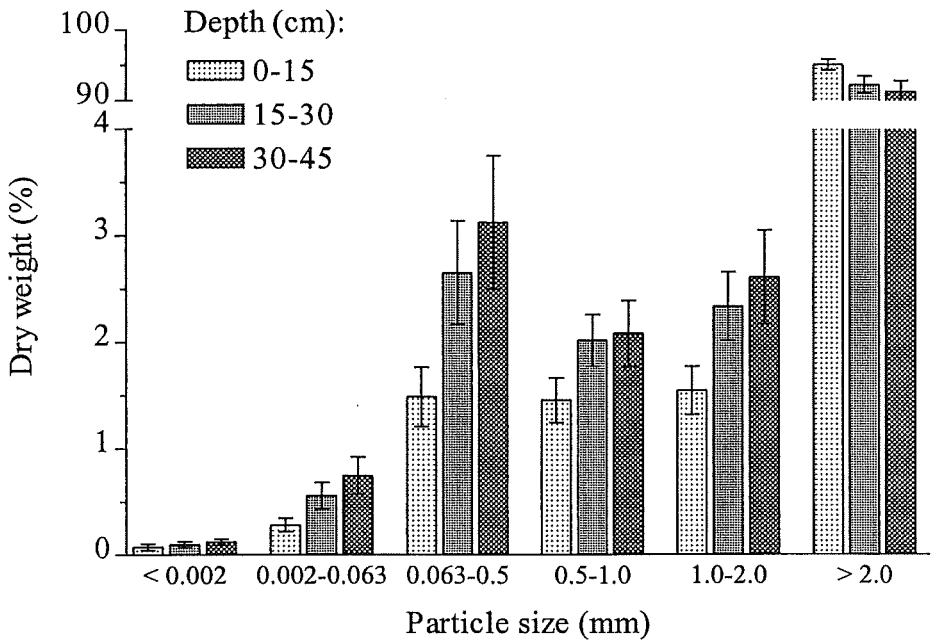

Figure 1. Mean (± 1 SE) substrate composition at three depths in hyporheic colonisation pots after four weeks in the Waipara River.

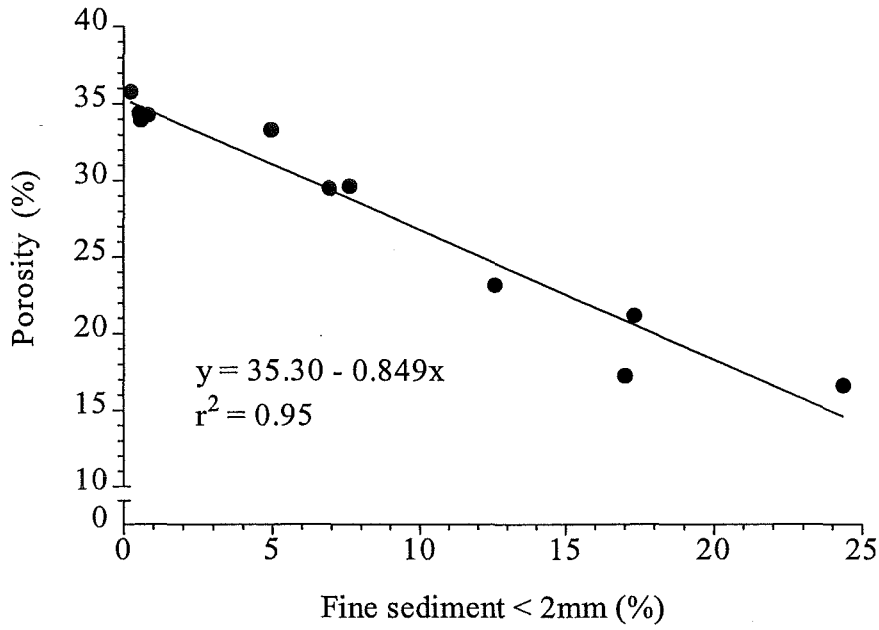

Figure 2. Relationship between sediment porosity (%) and the concentration of interstitial fine sediment < 2mm diameter.

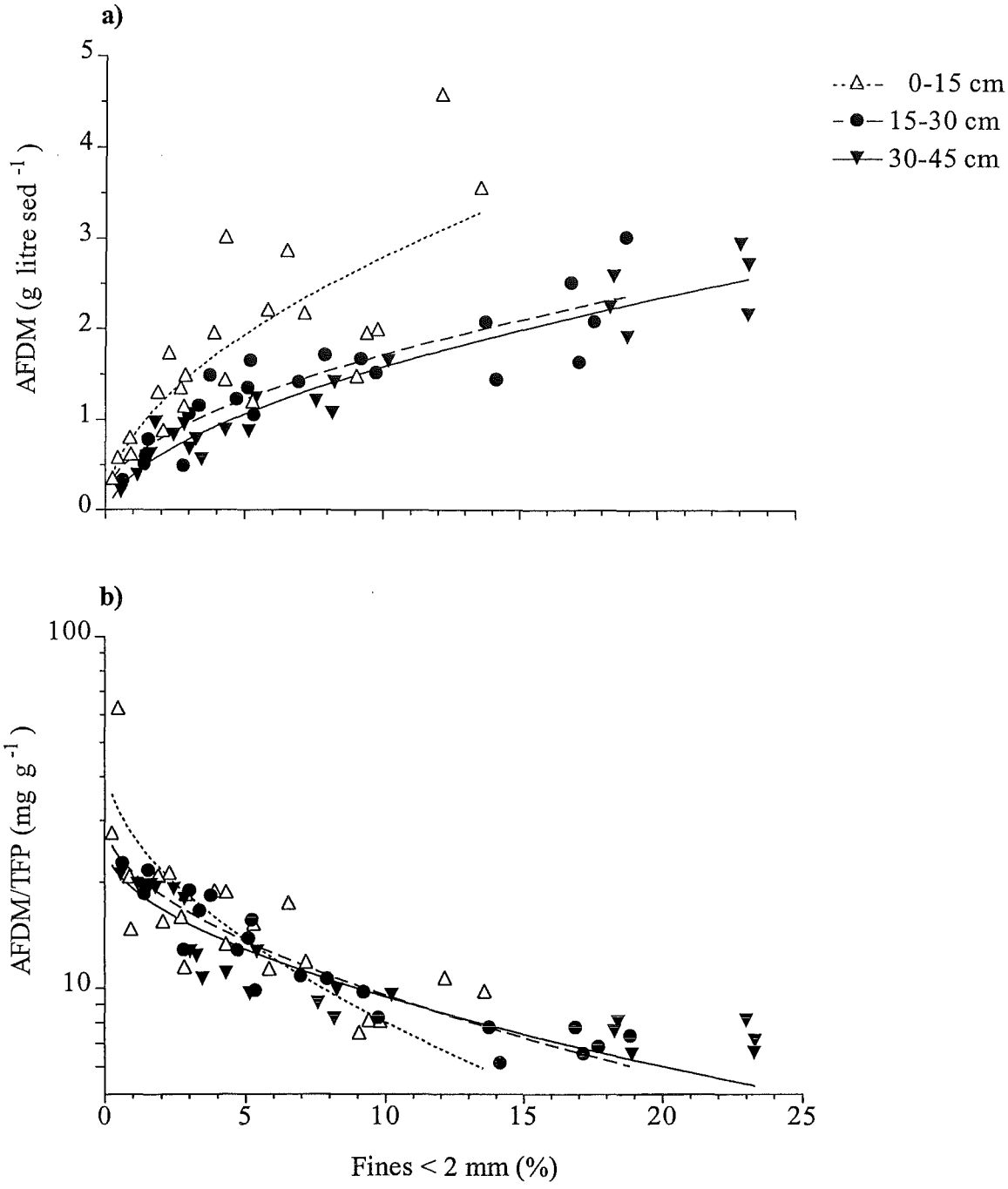

Figure 3. a) Ash-free dry mass (AFDM) and b) AFDM/total fine particles < 2mm diameter (AFDM/TFP) plotted against the percentage of fine sediment < 2 mm diameter in hyporheic colonisation pots (% dry weight) after four weeks in the Waipara River. Data for 3 substrate depths are shown along with non-linear regression curves (see methods for data transformations).

negatively affected by increased fines at 0-15 cm than at depths below 15 cm (ANCOVA depth x sediment interaction, $P < 0.05$, Figure 3b).

Community respiration & cellulolytic activity

Mean community respiration declined from 0.56 mg O_2 litre sed.$^{-1}$ hr^{-1} at 0-15 cm depth to 0.27 and 0.22 mg O_2 litre sed.$^{-1}$ hr^{-1} at 15-30 cm and 30-45 cm, respectively (Figure 4a). Community respiration was also negatively affected by interstitial fine sediment at all depths ($r^2 = 0.20$, $P < 0.001$). An increase in fine sediment concentration from 1 to 13.5% (the maximum concentration at 0-15 cm depth), resulted in a reduction in community respiration by 7% in shallow sediments (0-15 cm), 30% at 15-30 depth, and 43% at 30-45 cm.

Cotton tensile strength loss (CTSL) declined slightly, but significantly with depth ($F = 3.65$, $P = 0.03$), and was weakly, but positively associated with the concentration of fines ($r^2 = 0.07$, $P = 0.03$, Figure 4b). Mean CTSL was 0.104 kN at 0-15 cm and 0.083 kN at 30-45 cm. The average time taken for 50% loss of cotton tensile strength (CT50) was 42 days and ranged from 26-71 days. The average CT50 increased from 37 days at 0-15 cm to 46 days at 30-45 cm depth.

Invertebrate community

A total of 26 030 invertebrates, representing 38 identifiable taxa, were collected from 72 hyporheic samples. Ostracods dominated the fauna, numerically and made up 38% of all individuals collected. Ostracods, oligochaetes, the elmid beetle *Hydora* sp., and the hydrobiid snail *Potamopyrgus antipodarum* were found in all samples. Another 12 taxa were found in over half the samples (Table 1). Insects comprised only 26% of total invertebrate abundance.

On average, 19 taxa were collected per litre at 0-15 cm depth, while 16 and 15 taxa were collected per litre of sediment at 15-30 cm and 30-45 cm, respectively. Taxon richness was unaffected by fines concentration (ANCOVA $r^2 = 0.04$, $P = 0.08$).

Mean invertebrate abundance (all taxa combined) declined from 552 individuals per litre of sediment at 0-15 cm to 336 and 196 per litre at 15-30 cm and 30-45 cm, respectively (Figure 5). In addition, invertebrate abundance was positively correlated with interstitial fines at 0-15 cm, but was negatively correlated with fines below this depth

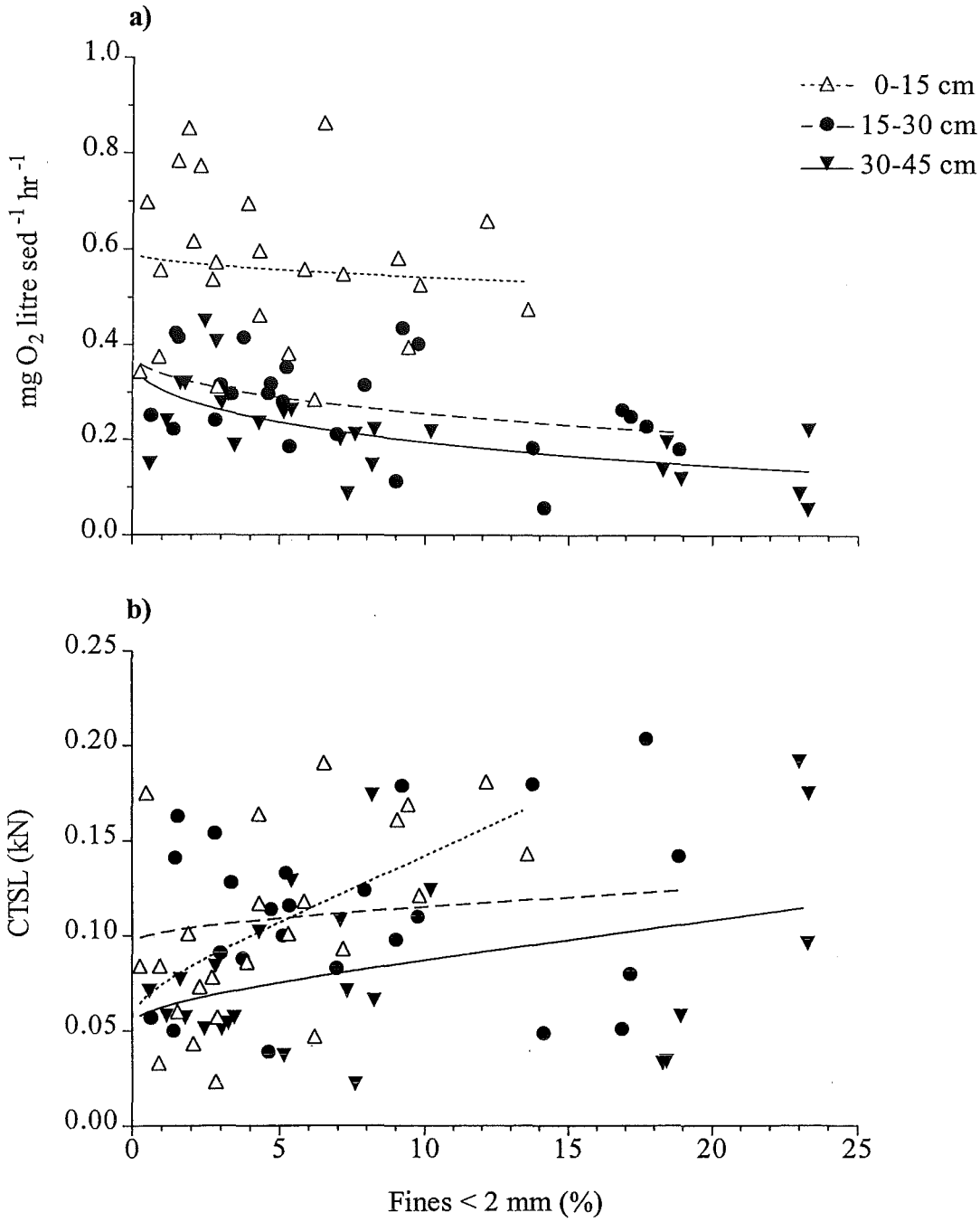

Figure 4. a) Community respiration and b) cotton strip tensile strength loss (CTSL) plotted against the percentage of fine sediment < 2 mm diameter in hyporheic colonisation pots after four weeks in the Waipara River. Data for 3 substrate depths are shown along with non-linear regression curves (see methods for data transformations).

Table 1. Mean abundance, percent frequency of occurrence and ANCOVA results comparing the effects of depth and fine sediment concentration (< 2 mm) on the most abundant hyporheic invertebrates collected in colonisation pot samples (0-45 cm deep) from the Waipara River. Arrows indicate an increase (⇧) or decrease (⇩) in invertebrate abundance associated with increased depth or fine sediment concentration. * = P < 0.05, ** = P < 0.01, *** = P < 0.001. P-values near statistical significance (0.05) are shown.

Taxon	Mean Density	Frequency	Depth		Fine sediment (%)			Depth x Sediment
	(No. l^{-1})	(%)	P	Effect	r^2	P	Effect	P
Ostracoda	138.5	100.0	***	⇩	—	ns	—	ns
Potamopyrgus antipodarum (Mollusca: Hydrobiidae)	55.5	100.0	***	⇩	0.23	***	⇩	ns
Hydora sp. (larvae) (Coleoptera: Elmidae)	55.0	100.0	***	⇩	0.06	*	⇩	**
Oligochaeta	50.6	100.0	ns	—	—	ns	—	*
Tanypodinae (Diptera: Chironomidae)	26.0	94.2	***	⇩	0.14	**	⇩	ns
Hydra sp. (Cnidaria)	6.8	65.2	*	⇧	0.31	***	⇩	ns
Deleatidium sp. (Ephemeroptera: Leptophlebiidae)	5.0	88.4	***	⇩	0.13	**	⇩	ns
Acari sp. 'G' (Acari)	4.4	78.3	ns	—	0.06	*	⇧	*
Chironominae (Diptera: Chironomidae)	3.7	72.5	**	⇩	0.12	**	⇩	ns
Tardigrada	3.3	73.9	*	⇩	—	ns	—	ns
Cyclopoida	3.0	78.3	ns	—	—	ns	—	ns
Orthocladiinae (Diptera: Chironomidae)	2.5	65.2	***	⇩	—	ns	—	ns
Nematoda	2.5	78.3	ns	—	—	ns	—	ns
Limnesia sp. (Acari: Limnesiidae)	2.2	60.9	ns	—	—	ns	—	ns
Acari larvae	1.7	42.0	*	⇧⇩	0.22	***	⇧	ns
Hydora sp. (adults) (Coleoptera: Elmidae)	1.6	59.4	**	⇩	0.05	0.051	⇩	ns
Aoteapsyche sp. (Trichoptera: Hydropsychidae)	1.4	50.7	***	⇩	—	ns	—	ns

(ANCOVA depth x sediment interaction, $P = 0.02$). Thus, an increase of interstitial fines from 1 to 13.5% increased mean invertebrate abundance by 86% at 0-15 cm, while the same increase in fines reduced invertebrate abundance by 30% at 30-45 cm depth.

Abundance of the elmid beetle *Hydora* sp. also increased with an increase in fines in the shallow sediments, but was negatively associated with fines below 15 cm depth (Figure 5, Table 1). Abundance of the hydrobiid snail, *Potamopyrgus antipodarum*, two subfamilies of chironomids, and the leptophlebiid mayfly *Deleatidium* sp., declined with depth and with increasing concentration of interstitial fines (Figure 5, Table 1).

Sediment effects were not limited to epigean taxa, although the abundance of only one hypogean taxon was negatively affected by the concentration of fines (Figure 6). *Hydra* sp. was most abundant at depths below 15 cm, and was strongly affected by increased fine sediment. Thus, *Hydra* density at 15-30 cm averaged 26 individuals per litre with 1% fines added, but only 2 individuals per litre with 13.5% fines added.

Oligochaetes and an unidentified mite (Acari sp 'G') were positively associated with interstitial fines at 0-15 cm, but not in deeper sediments (ANCOVA depth x sediment interaction, $P < 0.05$, Figure 6). Acari larvae were least abundant below 30 cm depth, and were the only group whose abundance increased across all depths with increasing concentration of fines (Figure 6, Table 1).

The abundance of epigean and insect taxa per litre of sediment declined with increasing fine sediment concentration at depths below 15 cm. However, the proportion of total invertebrate abundance composed of epigean and insect taxa was negatively associated with fines concentration at all depths (Figure 7, Table 2). In contrast, the density of hypogean taxa per litre increased with fines concentration at 0-15 cm, but showed little relationship with fines at depths below 15 cm (Figure 7).

Meiofauna comprised 66% of the total invertebrate fauna and 48% of insects could be categorised as meiofauna. Meiofauna were slightly ($F = 2.85$, $P = 0.06$) more abundant at 15-30 cm (70% of total abundance) than at 30-45 cm (62%). However, fine sediment concentration did not affect the proportion of total fauna, or insect fauna, made up of meiofauna (Table 2).

Ordination of invertebrate assemblages found in pots in the Waipara River revealed no trend in composition associated with fine sediment concentration at 0-15 cm (Figure 8). However, with increasing depth, assemblage composition diverged in samples differing in concentration of fines. Percent fines < 2 mm was positively correlated with axis 1 ($r_s = 0.36$, $P = 0.002$) and axis 2 ($r_s = 0.63$, $P < 0.0001$). An overall decrease in invertebrate

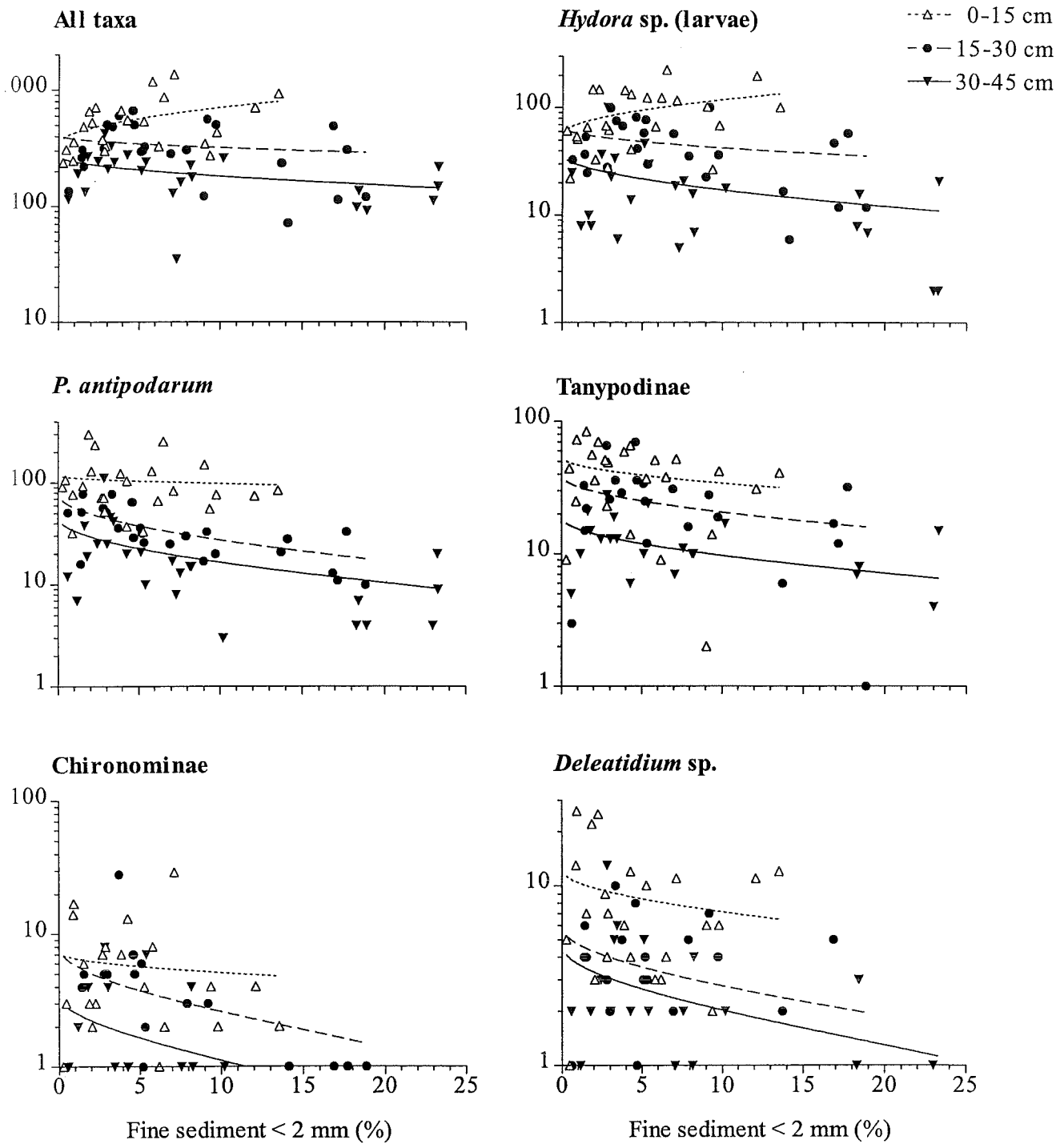

Figure 5. Relationships between abundances of all invertebrates, selected epigean taxa, and the percentage of fine sediment < 2 mm diameter in hyporheic colonisation pots after four weeks in the Waipara River. Data for 3 substrate depths are shown along with non-linear regression curves (see methods for data transformations).

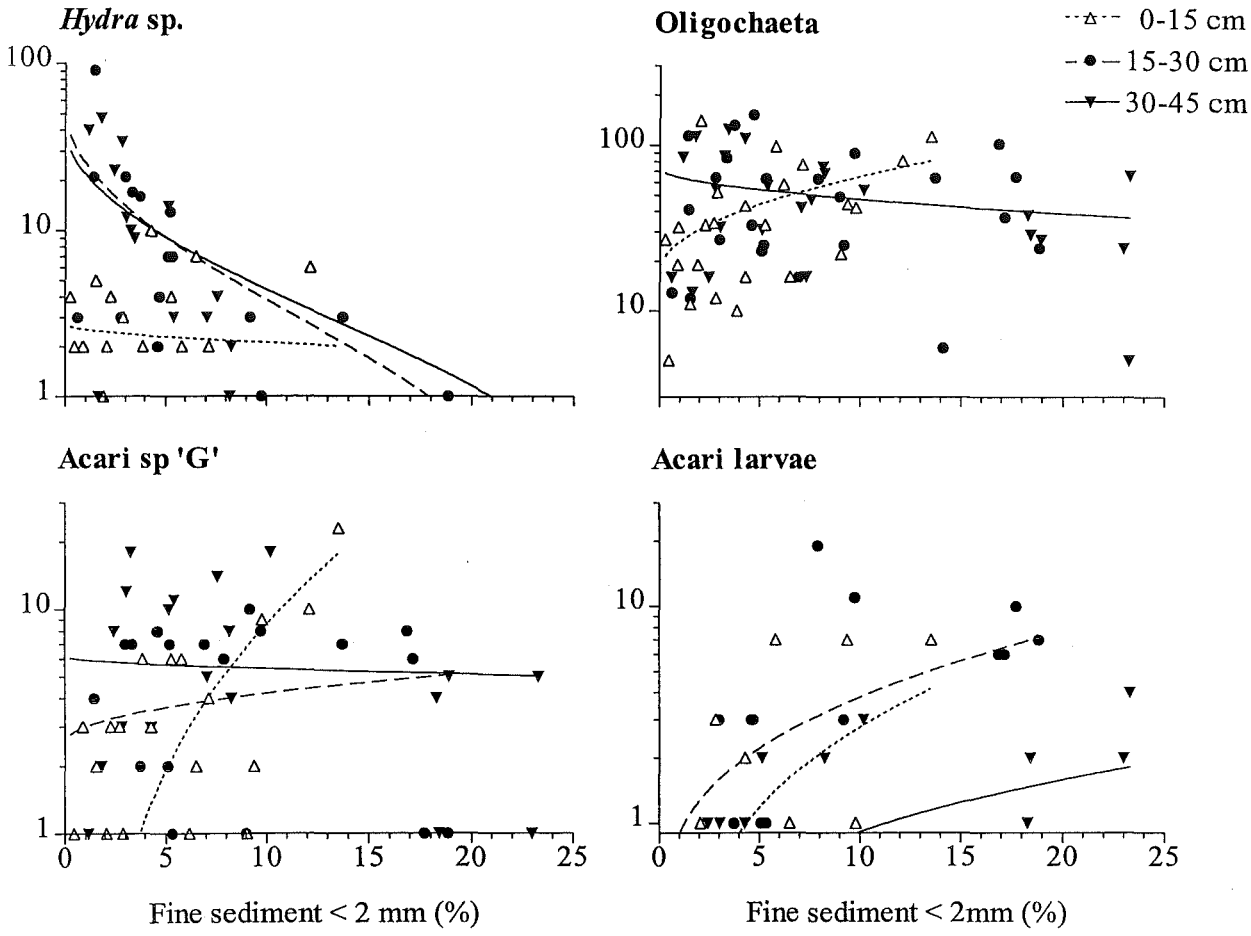

Figure 6. Relationships between abundances of selected hypogean taxa and the percentage of fine sediment < 2 mm diameter in hyporheic colonisation pots after four weeks in the Waipara River. Data for 3 substrate depths are shown along with non-linear regression curves (see methods for data transformations).

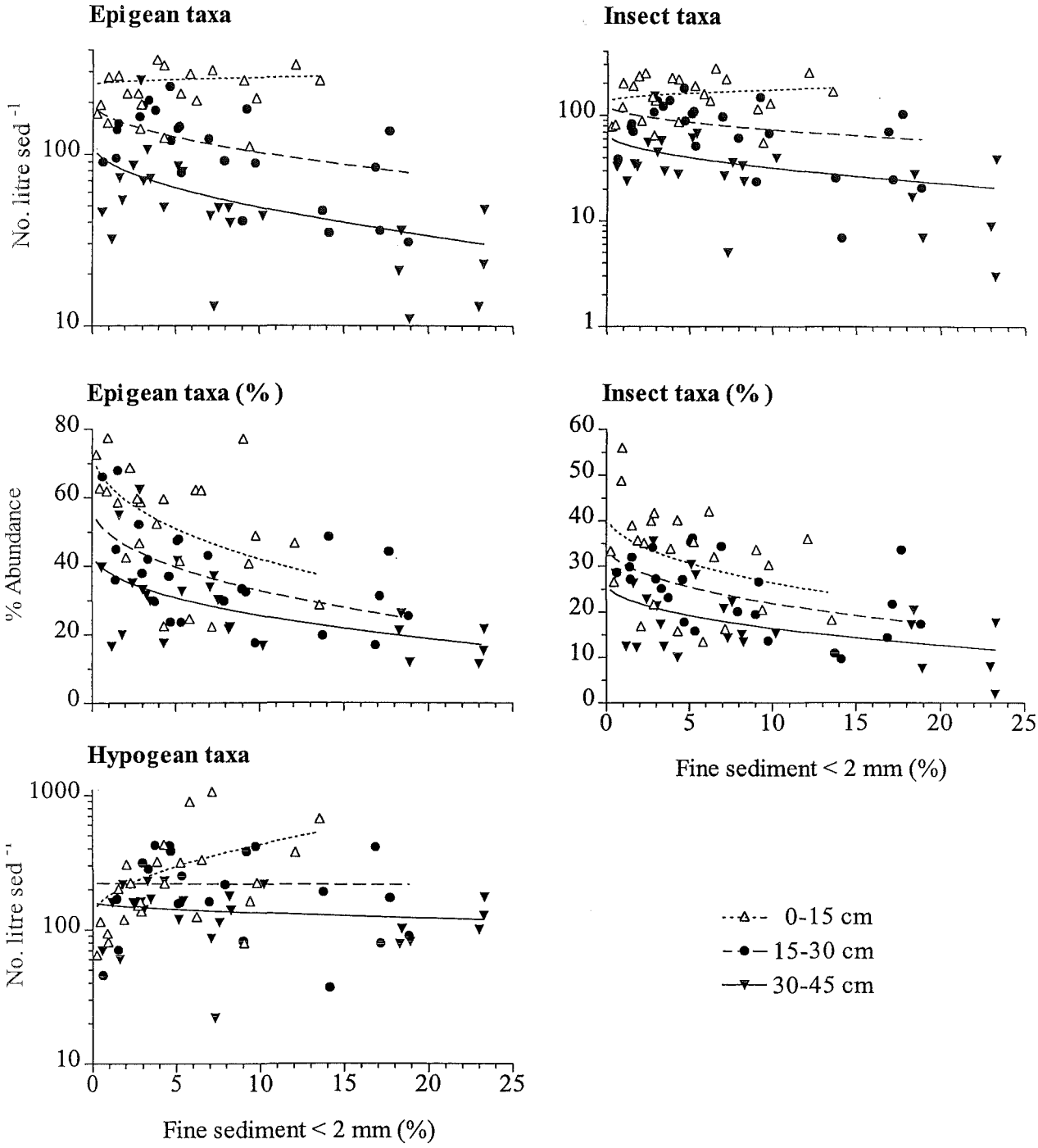

Figure 7. Relationships between abundances of selected invertebrate taxa and the percentage of fine sediment < 2 mm diameter in hyporheic colonisation pots after four weeks in the Waipara River. Data for 3 substrate depths are shown along with non-linear regression curves (see methods for data transformations).

Table 2. Results of ANCOVA testing the effects of depth and fine sediment (< 2 mm) concentration on the abundance of seven invertebrate groups. Arrows indicate whether metrics increase (⇧) or decrease (⇩) in response to increasing depth or fine sediment concentration. * = P < 0.05, ** = P < 0.01, *** = P < 0.001. One P-value near statistical significance (0.05) is also shown.

Response variable	Depth		Sediment			Depth x Sediment
	P	Effect	r^2	P	Effect	P
Epigean taxa (abundance l^{-1})	***	⇩	0.28	***	⇩	ns
Insects (abundance l^{-1})	***	⇩	0.16	***	⇩	*
Hypogean taxa (abundance l^{-1})	**	⇩	0.12	**	⇧	ns
Epigean taxa (%)	***	⇩	0.25	***	⇩	ns
Insects (%)	***	⇩	0.21	***	⇩	ns
Meiofauna (%)	0.06	⇧⇩	—	ns	—	ns
Insect meiofauna (%)[†]	ns	—	—	ns	—	ns

[†] The percentage of all insects that were meiofauna

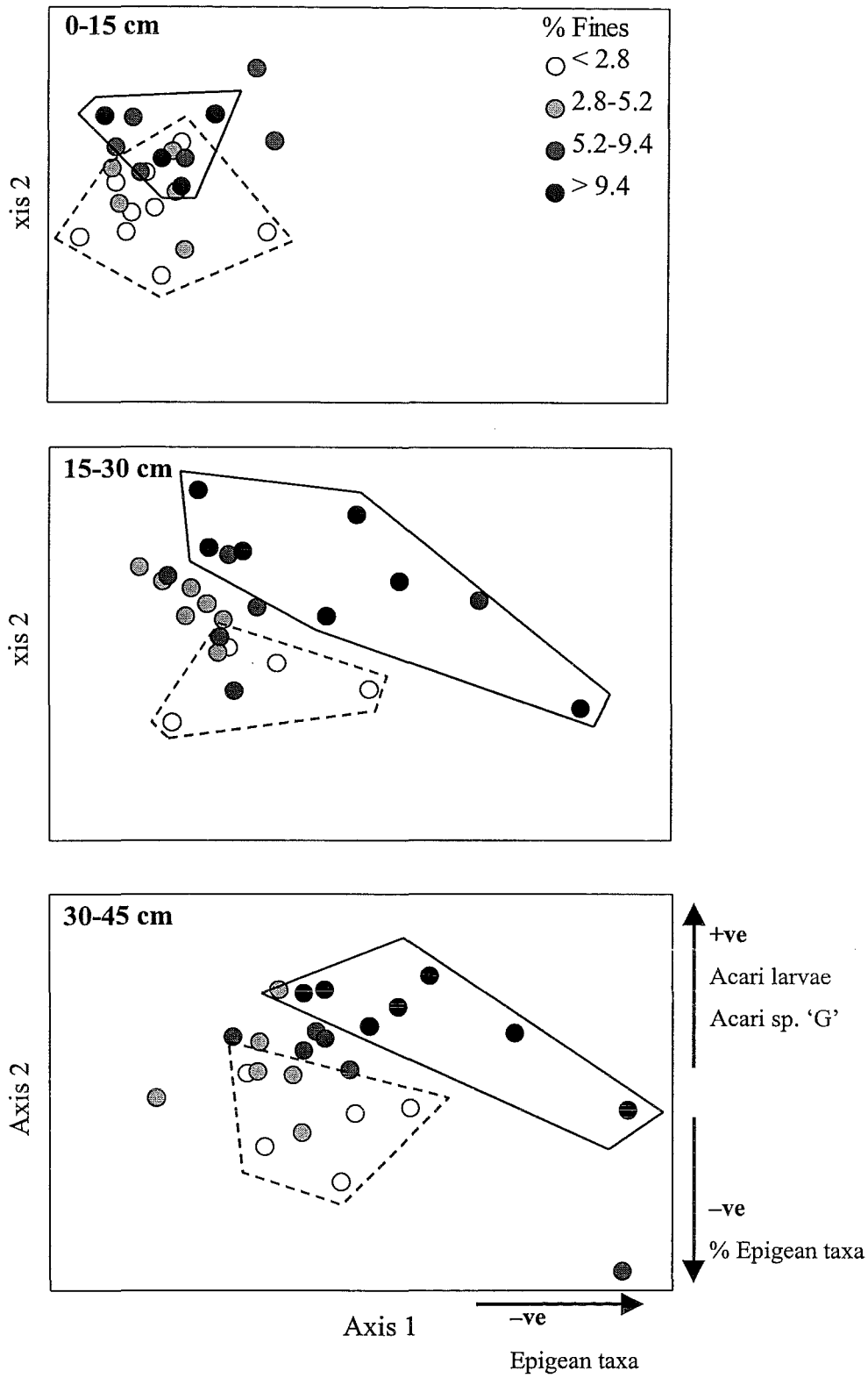

Figure 8. MDS ordination (stress = 0.19) of invertebrates at three depths collected from colonisation pots after four weeks in the Waipara River. Symbols indicate the concentration of interstitial fine sediment < 2 mm in each sample (25% of samples are in each category). Polygons enclose samples with the lowest (dashed line) and highest (solid line) fine sediment concentration. Invertebrate taxa correlated with axis scores are shown.

abundance was associated with a shift from left to right on axis 1 and was especially pronounced for epigean taxa, (r_s = -0.91, P < 0.0001). Axis 2 scores were positively correlated with the abundance of larval mites (r_s = 0.67, P < 0.0001) and an unidentified mite (Acari sp 'G'; r_s = 0.44, P < 0.0001), and negatively correlated with the proportion of the fauna composed of epigean taxa (r_s = -0.48, P < 0.0001).

Discussion

Invertebrate responses to fine sediment addition

Increased concentrations of interstitial fines resulted in reduced community respiration and lower invertebrate abundance, especially of epigean taxa. These findings support my initial hypothesis, and are in agreement with the work of others (Ward & Palmer, 1994; Strayer et al., 1997; Brunke & Gonser, 1999) that fine sediment concentration is an important determinant of hyporheic community structure. The abundant epigean taxa *Hydora* sp. (Elmidae), *Potamopyrgus antipodarum*, Chironomidae and the mayfly *Deleatidium* sp., are all common and widely distributed in New Zealand streams and rivers (Quinn & Hickey, 1990), and results of my experiment indicate they are sensitive to fines in the hyporheic zone.

The abundance of oligochaetes, ostracods and tardigrades, and total invertebrate abundance were positively correlated with interstitial silt content at all depths in a food limitation experiment described in Chapter 4, but not in the present experiment. In fact, only one invertebrate group (larval mites) showed a positive correlation with fine sediment at all depths. However, the range of silt entrained by colonisation pots in the earlier study (0.2 – 2.3 g per litre of sediment) was considerably lower than in this experiment (0.5 – 64.5 g l^{-1}), indicating that effects on the invertebrate community were concentration-dependent. That being the case, my data provide support for Collier & Scarsbrook's (2000) prediction of a 'subsidy-stress' (sensu Odum et al., 1979) type relationship between fine sediment and invertebrate abundance in the hyporheic zone. Thus, low concentrations of interstitial silt may enhance the food supply of some taxa (an ecosystem 'subsidy'), whilst higher levels of silt may lower invertebrate abundance due to reduced sediment porosity and oxygen supply (an ecosystem 'stress').

The effects of fine sediment on invertebrate density were not consistent at all depths for all taxa, although a negative association with fines was more common below 15 cm. This suggests that the sensitivity of interstitial invertebrates to fine sediment increased with depth. A possible explanation for this is that the effects of fine sediment on the penetration of surface water are offset in shallower sediments by the higher rate of water and oxygen exchange with surface water. This seems particularly likely, given that oxygen concentration typically declines more rapidly with depth in fine sediments (Jansson, 1967; Whitman & Clark, 1982; Metzler & Smock, 1990; Boulton et al., 1992) than coarse sediments (Stanford & Ward, 1988; Dole-Olivier & Marmonier, 1992; Brunke & Gonser, 1999). In addition, greater compaction of the sediment may have occurred with depth, due to the mass of overlying sediment further reducing sediment permeability to channel water and dissolved oxygen.

Ryder (1989) found that the density of some benthic invertebrates (< 10 cm depth), particularly *Deleatidium*, declined in response to experimental additions of fine sediment < 1 mm diameter in two Otago streams, but that oligochaetes, elmids and *P. antipodarum* were unaffected. In a second experimental study undertaken in the North Island of New Zealand, Dunning (1998) found a lower proportion of mayflies, and a greater proportion of Coleoptera (including Elmidae), Diptera and Mollusca in treatments (< 10 cm depth) containing high sediment concentrations. These findings suggest that elmids and *P. antipodarum* are relatively tolerant of fine sediments, yet in my experiment they were sensitive to fine sediment additions within the hyporheic zone. The disparity between my findings and those of Ryder (1989) and Dunning (1998) indicate that the effects of fine sediment can differ at different depths within the stream bed. Sediment deposition can affect benthic invertebrates by reducing epilithic food quality, clogging respiratory structures, reducing filter feeding efficiency, and increasing oxygen demand (Wood & Armitage, 1997). Fine sediment may also reduce interstitial flow rates (Angradi, 1999), resulting in a poorer supply of dissolved oxygen to the hyporheic zone (Jansson, 1967; Hynes, 1974). Hyporheic invertebrates may actively avoid poorly oxygenated regions of sediment (Henry & Danielopol, 1999), and it seems likely that lowered hyporheic dissolved oxygen, caused by fine sediment deposition, creates an environment that is unfavourable to epigean taxa, which are relatively tolerant of fine sediment in benthic sediments. Thus, fine sediment may exert a stronger negative influence on invertebrate abundance in the hyporheic zone than at or near the surface of the stream bed.

Microbial activity

Hyporheic community respiration (CR) can make a major contribution to overall stream metabolism. In my experiment, the hyporheic zone (15-45 cm) accounted for about 47 % of total sediment respiration, and therefore was within the 40-96 % range reported elsewhere (Pusch & Schwoerbel, 1994; Mulholland et al., 1997; Naegeli & Uehlinger, 1997). Furthermore, hyporheic community respiration was reduced in the presence of fine sediment in the Waipara, again consistent with other research findings. Thus, Jones (1995), Dodds et al. (1996) and Alfrieder (1997) found that fine substrata supported lower microbial activity than coarse subsurface substrata.

In contrast to community respiration, cellulose decomposition, measured as cotton tensile strength loss (CTSL), showed a weak positive correlation with the concentration of interstitial fines. The average time taken for 50% loss of cotton tensile strength (CT50) in the Waipara was 42 days and fell between the CT50 values reported by Boulton & Quinn (2000) for floodplain sediments of the Rhône River in France (34-124 days) and the hyporheic zone of several streams near Hamilton, New Zealand (9-20 days). Boulton & Quinn (2000) found greater decomposition rates in fine than coarse sediments in downwelling zones of the Rhône. However, they found that cellulose decomposition was lower in upwelling zones than downwelling zones in several New Zealand hill country streams affected by silt deposition. The interplay between vertical hydrologic exchange, sedimentation and decomposition were not investigated in my study, which was conducted in a uniformly downwelling run.

Differences in microbial activity inferred from CR and CTSL may be due in part to the different microbial processes they reflect. I measured CR as oxygen uptake, which therefore represented the combined aerobic activity of invertebrates and a suite of microbes, including bacteria, fungi and protozoa. Pusch & Schwoerbel (1994) attributed over 90% of hyporheic CR to organisms < 100 μm long in an alpine stream in Germany, but it is not known which of these diverse groups contributed most to CR in the Waipara. Although oxygen uptake of sediments measures aerobic metazoan and microbial activity, cellulose decomposition is a microbial process and can be either aerobic or anaerobic (Howard, 1988). In aerobic aquatic sediments, cellulose is broken down mainly by myxobacteria and higher fungi (particularly hyphomycetes), whereas clostridia are the main decomposers of cellulose in anaerobic conditions (Rheinheimer, 1992).

Another difference between my two measures of microbial activity is that while CR is an instantaneous measure of activity, the cotton strip assay integrates in situ decomposition over time (Latter & Walton, 1988). Furthermore, it may not be a linear process and much of the loss of cotton tensile strength may occur during the initial stages of microbial colonisation (Smith & Maw, 1988). Therefore, although CR was negatively affected by fine sediment concentration at the end of the experiment, the weak positive relationship between fines and CTSL suggests that the effect of fines on microbial activity was not constant throughout the course of the experiment. As a slight increase in fine sediment concentration with depth was evident at the end of the experiment, it was also apparent that conditions in the colonisation pots changed over time. Other factors, such as the degree of sediment packing or compaction may also have increased with time, causing microbial activity to decline.

Application of experimental results

Fine sediment may smother underlying sediments (colmation) or filter down through them (depth filtration), resulting an increase in fines with depth (Naegeli et al., 1995; Brunke, 1999). In the Waipara experiment, fines tended to increase in concentration with depth, suggesting that depth filtration was more prevalent than colmation. Since depth filtration does not result in clogging the surface layer of sediment (Brunke, 1999), its effects on the hyporheic community may be considerably less than those of colmation, which is likely to result in a greater reduction in interstitial flow and oxygen concentration. Colmation is most likely to occur where low flow is coupled with a high rate of fine sediment deposition, whereas depth filtration seems more likely to occur when the rate and amount of sediment deposition is lower (Brunke, 1999).

Manipulations of small patches of sediment, as achieved in this experiment, do not simulate the effects of sedimentation on a whole stream reach or catchment (Angradi, 1999), and do not provide insights into the long-term ramifications of sedimentation. Indeed, Harding et al. (1998) showed that the deleterious effects of forest clearance on benthic stream invertebrates may extend for over 50 years after return to a forested condition, and suggested that the benthic fauna may never recover. Results from the Waipara may therefore be seen as a 'best case scenario' for sediment effects on the hyporheos, since larger scale sediment additions are likely to result in more widespread impacts on the biota.

The value of my results is that they provide data on the influence of fine sediment on hyporheic communities, without confounding site-to-site variability that may occur when comparing effects among different streams (Strayer et al., 1997; Angradi, 1999). The data also provide information on the relative effects of fines at different depths, and on different members of the interstitial community. As such, they may be helpful in interpreting the results of other studies.

For example, Quinn et al. (1992) found the abundance of most benthic invertebrate taxa declined downstream of placer gold mining operations in six streams on the West Coast of the South Island. Lower epilithic biomass and degraded epilithic food quality caused by increased turbidity and clay deposition, were the likely reasons for low invertebrate densities at downstream sites (Quinn et al., 1992). However, lower interstitial permeability (at 0.3 m) and lower dissolved oxygen concentrations were also found at some sites, which may also be implicated in the reduction of downstream benthic invertebrate densities. Results from my experiment suggest reduced sediment permeability at the West Coast sites also would have significantly reduced CR and invertebrate abundance in the hyporheic zone. Finally, it is interesting to note that the only taxon to increase in abundance downstream of mining discharges was *Hydora* (Quinn et al., 1992). My results suggest that this would not have been the case in the hyporheic zone, and that the effect of fine sediment on *Hydora* larval abundance in the West Coast streams may have been positive near the sediment surface, but negative at depth.

In summary, addition of fine sediment to hyporheic colonisation pots reduced microbial activity and the abundance of epigean invertebrates in the Waipara River. The hyporheic invertebrate community (below 15 cm depth) showed greater sensitivity to fine sediment inputs than the benthic community (above 15 cm). These findings indicate that the deleterious effects of fine sediment on river communities may extend beyond the depth reached by standard benthic sampling, and that sampling to a greater depth is likely to reveal impacts on communities that may not be apparent in shallower sediments.

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Chapter 7

Summary and discussion

Research summary

The aim of this thesis was to determine what factors limit the abundance and composition of hyporheic invertebrate and microbial communities in several Canterbury rivers, using field surveys in association with field and laboratory experiments.

The role of hydrology in structuring hyporheic communities was investigated in Chapters 2 and 3. Data from these chapters indicate that the hyporheos may be seasonally limited by dissolved oxygen (DO) concentration, depending on the vertical hydraulic gradient (VHG). Upwelling hydrologic conditions resulted in lower DO concentrations in summer (minimum concentration = 2 mg l^{-1}), but greater infiltration of DO-rich channel water during high flows in winter reduced the negative effect of upwellings on invertebrate abundance.

All four rivers sampled contained reaches with intermittent flow, which resulted in a distinct invertebrate fauna dominated by collembolans (where no flow was present) or harpacticoid copepods (in saturated sediments immediately upstream of the dry stream terminus). All rivers sampled contained abundant and diverse hyporheic and epigean invertebrate faunas. A new species of isopod was discovered (*Heterias* sp., Janiridae), and numerous mites and crustaceans that could not be identified were abundant. The apparent composition of the fauna was influenced strongly by sampling method, with colonisation pots biased towards epigean taxa such as the snail *P. antipodarum*, whereas pump-sampling was biased towards collecting small crustaceans and mites.

Invertebrate abundance was positively correlated with organic matter content and negatively correlated with fine sediment concentration (inferred from the turbidity of pumped water) of colonisation pot sediments in the Waipara. A field manipulation of leaves in colonisation pots (Chapter 4) resulted in an increase in overall invertebrate abundance and community respiration, although the effect of leaves declined with depth. However, abundance of ostracods increased in response to leaf addition at all depths and it appears these detritivores are able to discriminate between patches of low and high resource availability regardless of depth. Invertebrate community composition was found

to be related to the concentration of fine sediment (< 63 μm) in colonisation pots suggesting that low concentrations of fine sediment (< 2.5 g silt per litre of sediment) may interfere with the ability of some taxa (mainly grazers) to feed, whilst providing an organic substrate for burrowers and collector-filterers.

The epilithic microbial community on cobbles incubated in the hyporheic zone was similar to that of heavily-shaded surface epilithon, and had lower biomass and a less diverse microbiota than epilithon grown in the light (Chapter 5). The epigean caddisfly, *Olinga feredayi*, which is often found in the hyporheic zone, ingested hyporheic epilithon, but did not grow in the absence of either higher quality light-grown epilithon, or coarse particulate organic matter (CPOM). In addition, larvae fed hyporheic biofilms with fine particulate organic matter (FPOM) added were in poorer condition than those fed light-grown biofilms and CPOM. Larvae of *O. feredayi* probably move among patches of high and low quality food within the hyporheic zone and at the substrate surface.

The addition of fine sediment (< 2 mm diameter) to colonisation pots containing gravel reduced invertebrate abundance and community respiration (CR) at all depths (0-45 cm). Invertebrate community composition was affected more strongly by fine sediment at depths below 15 cm, indicating that conventional stream sampling may provide an inadequate measure of sediment effects on the benthos.

Implications of the research findings

Biodiversity

The Waipara River, and the three tributaries of the Ashley River all harboured an abundant and diverse hyporheic fauna. During a pilot study in February 1997, pump-sampling of a further three tributaries of the Ashley River (Karetu Creek, Okuku River and Wooded Gully Stream) also revealed an abundant hyporheic fauna dominated by mites and copepods. Unfortunately, most of these mites could not be identified beyond morpho-species, and the particularly abundant Harpactacoida were not identified beyond order. Little is known of New Zealand's subsurface fauna, although taxonomic work to date indicates it may be diverse. For example, Cook (1983) described 73 new water mites, including 37 hyporheic species, from a number of New Zealand rivers, following a two month collecting trip. In addition, it is thought that 10 new genera of groundwater

amphipods containing at least 28 new species occur in New Zealand (Collier, 2001). In a recent paper, Collier et al. (2000) reported the collection of 188 different stream invertebrate taxa from 24 sites within the Mangaotama Stream catchment (North Island) over a 7 year period, the greatest number of taxa identified in a single New Zealand river system. Of the 188 taxa, hyporheic sampling (colonisation pots, freeze-coring and pump-sampling) yielded 11 that were not taken by other sampling methods (adult trapping and benthic Surber sampling). However, the contribution of subsurface diversity to whole-river diversity is hampered by inadequate taxonomy, so 11 is almost certainly an underestimate. Given the high degree of endemism of the New Zealand invertebrate fauna, and the restricted nature of the habitats in which numerous groundwater invertebrates have been found (Collier, 1993), subsurface waters are likely to provide important sources of new taxa and well worth further study. As an example of how increased taxonomic resolution can influence biodiversity estimates, identification of the meiofauna (predominantly chironomids and rotifers) of Broadstone Stream in Southern England increased the number of benthic taxa present 5-fold, from 24 to 130 (Schmid-Araya & Schmid, 2000). Although many meiofaunal groups are likely to be biofilm grazers or detritivores, there are also numerous predators, which may contribute significantly to food web dynamics (Schmid & Schmid-Araya, 1997; Schmid-Araya & Schmid, 2000). In the Oberer Seebach, in Austria, 97 prey species (mostly rotifers and chironomids) were identified from the guts of two species of Tanypodinae (Chironomidae) (Schmid & Schmid-Araya, 1997; Schmid-Araya & Schmid, 2000). Tanypods formed a large proportion of hyporheic invertebrate biomass in the Ashley River tributaries I studied, but the identities of their prey are as yet unknown. Simlarly, small polycentropodid caddisfly larvae were also common in the hyporheic zone of Ashley River tributaries, and may be important predators. On several occasions, fine gravel particles withdrawn by pump-sampling had fragments of silken nets attached, possibly spun by polycentropodids that were feeding in the hyporheic zone. Clearly, the inclusion of permanent and occasional hyporheic invertebrates, including meiofauna (Hakenkamp & Morin, 2000; Robertson et al., 2000) in food web studies has the potential to dramatically increase our understanding of community structure and function.

Ecosystem processes, human impacts and management

Results obtained in my research support the concept of the hyporheic zone as a dynamic ecotone (Gibert et al., 1990; Vervier et al., 1992) between surface water and groundwater. Thus, in upland or constrained valley reaches, upwelling conditions resulted in seasonal reductions in dissolved oxygen associated with lower invertebrate abundance. In addition, finer, and less permeable sediments were associated with lower invertebrate abundance and community respiration. The rate and direction of hydrologic exchange also influence nutrient dynamics in the hyporheic zone, as shown by Duff & Triska (2000) who found that well-oxygenated sediment interstices promote aerobic metabolism and nitrification, while low hydraulic conductivity and high rates of metabolic activity may result in reduction of nitrate reduction. Hyporheic zones may serve to increase the retention of solutes in river reaches, through sediment adsorption and microbial activity (Triska et al., 1989; Mulholland et al., 1997; Valett et al., 1997), but this has yet to be studied in New Zealand. Nevertheless, human impacts on the hyporheic zone are most likely to be related to reductions in the rate of hydrologic exchange across the surface water-substrate ecotone, brought about by sedimentation or artificially reduced river flow (Brunke & Gonser, 1997; Boulton, 2000). In the Waipara River, a change in land use over the last decade from predominantly pastoral farming to intensive olive and grape growing has been associated with increased demand on groundwater resources (Loris, 2000). As numerous wells may be hydrologically linked to the river (Pattle Delamore Partners Ltd., 1996; Loris, 2000), increased groundwater use could reduce surface flow of the Waipara, potentially affecting aquatic communities. Although alluvial rivers such as the Waipara and others draining the Canterbury foothills may experience periods of intermittent flow unrelated to land use practises (Canterbury Regional Council, 1999), virtually nothing is known of the effect of flow intermittency on hyporheic communities other than my findings that an intermittent reach of the Waipara supported a less diverse invertebrate fauna, but similar community respiration to comparable, permanently flowing reaches. Studies of desert streams in North America (e.g., Valett, 1993; Stanley et al., 1994; Boulton & Stanley, 1995; Clinton et al., 1996) and Australia (e.g., Cooling & Boulton, 1993; Boulton & Brock, 1999) have shown that the hyporheic zone may be the main region of biological activity in the stream. This suggests that microbial and invertebrate communities may be affected differently by low flow, and that future research on low flow effects needs to incorporate both

communities in order to appreciate the effects of natural and human-induced low flow on river ecosystems.

Flow regulation and permanently lowered river flows may also reduce the incidence of flushing events that can remove fine sediment from within at least the upper portion of the hyporheic zone and maintain its permeability (Schälchli, 1992; Brunke & Gonser, 1997). Mining and farming may also enhance fine sediment deposition (Wood & Armitage, 1997) with consequences for the biota. I found that while small concentrations of fine sediment (< 2.5 g silt per litre of sediment) may stimulate the abundance of some burrowing and filter-feeding invertebrates, high concentrations of fine sediment reduced overall invertebrate abundance and community respiration. In addition, I found that hyporheic invertebrates may be more sensitive to fine sediment addition than many epigean species. While invertebrates such as oligochaetes or bivalves may aerate fine sediments by their burrowing activities (Vanek, 1997; Mermillod-Blondin et al., 2000; Vaughn & Hakenkamp, 2001), fine sediments can also adsorb heavy metals, adding to their toxicity to interstitial taxa (Gibert et al., 1995). Similarly, Lafont et al (1996) found that paper mill effluent was toxic to many hyporheic oligochaetes in the River Moselle, France, indicating that the hyporheic zone will not necessarily act as a refuge from pollution.

The hyporheic zone is clearly an integral part of a riverine ecosystem. It contains a rich invertebrate fauna, provides important sites for the retention and transformation of organic matter and nutrients, but may also be sensitive to human activities. Management of hyporheic zones in New Zealand falls within the domain of regional councils, who are responsible for the sustainable management of water resources (Canterbury Regional Council, 1999). However, while groundwater is tapped for municipal water supplies and irrigation in regions like Canterbury, regional environmental reports make no mention of the subsurface biota beyond groundwater contamination by faecal colliform bacteria (Canterbury Regional Council, 1996; Environment Canterbury, 2001). This is despite the groundwater fauna of Canterbury having been known of for over 100 years (Chilton, 1894; Sinton, 1984) and the early efforts of Chilton (1924) who wrote numerous newspaper articles urging Christchurch citizens to "...realise the value of the stores of water beneath your feet...".

Collier (1993) wrote that the greatest threat to New Zealand freshwater invertebrates is the loss and reduction of habitat by human activities. This contention applies to the hyporheos as well as the better known surface fauna, but as I have indicated

much basic information is lacking on subsurface communities at present. In the absence of region-specific biodiversity information, simple measures of microbial community activity or rates of hydrologic exchange as used in my research could be used to give an indication of the 'health' of hyporheic communities (Boulton, 2000). However, broader ecological research on subsurface nutrient dynamics, food webs, and effects of river flow and pollution sensitivity is needed.

Hynes (1983) urged stream biologists to consider the influence of interactions between streams and groundwater to create a better understanding of how stream communities function. The growing body of literature on hyporheic ecology worldwide indicates that contemporary stream ecologists have heard his plea (Valett et al., 1993; Stanley & Jones, 2000). It is now up to hydrologists and water managers to consider the biota of surface *and* subsurface waters concomitantly, so that freshwater ecosystems can be understood, maintained and protected, effectively.

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